Fraser, David (1998) *Trophic polymorphism in the Arctic charr (Salvelinnus alpinus (L.)) of Lochs Rannoch, Ericht and Tay, Scotland.* PhD thesis.

TROPHIC POLYMORPHISM IN THE ARCTIC CHARR (*Salvelinus alpinus* (L.)) OF LOCHS RANNOCH, ERICHT AND TAY, SCOTLAND.

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THIS THESIS IS SUBMITTED FOR THE DEGREE OF DOCTOR OF PHILOSOPHY

DIVISION OF ENVIRONMENTAL AND EVOLUTIONARY BIOLOGY,

INSTITUTE OF BIOMEDICAL AND LIFE SCIENCES

UNIVERSITY OF GLASGOW,

APRIL, 1998

ACKNOWLEDGEMENTS

There are a number of people to whom I owe thanks for their contribution to this study. Firstly, thank you to my supervisors, Colin Adams and Felicity Huntingford for entrusting me with the studentship in the first instance and for their subsequent guidance and advice throughout the study. It was a pleasure to work on a number of occasions, with Colin Bean, who also took a keen interest in and assisted with my work. The staff of the University Field Station, Rowardennan are thanked for their assistance during my time spent there.

The following people each gave up at least a day of their time to assist with field sampling and therefore deserve my thanks: Belen Calvo, Chris Cutts, Mark Bannan, Mustafa Dorucu, Kirstine O'Connor, Dave Stevens, Mark Cook, Steve Arnott, Alexandra Hay, Francis Neat, Colin Bull, Matt Cottam, Matt O'Hare, Emma Combes, Sveinn Valdimarsson, Alfredo Nicieza, Alasdair Knox, Natasha Hitchman, Dave Ridell and Dave Aird. Thank you also to my office mates, past and present namely Sveinn Valdimarsson, Colin Bull, Francis Neat and Kirstine O'Connor for putting up with me and Amanda MacLean for her spelling advice.

Access was kindly granted to Loch Rannoch by the Loch Rannoch Conservation Association, to Loch Ericht by Ralia, Talla Bheith, Ben Alder, Corrie Varkie and Camusericht Estates and to L. Tay by the Tay District Salmon Fisheries Board and Loch Tay Central Salmon Fishings Limited. The co-operation of all these parties was very much appreciated.

Janice Fletcher of the Institute of Freshwater Ecology, Windermere provided expert advice on otolith reading.

Siggi Snorsason and Skuli Skúlason were most hospitable during my stay in Iceland and as a result of time spent with them and Hilmar Malmquist I learned a great deal about charr.

Finally, thank you to Janet Holmes for putting up with me and my fish obsession, some of which has definitely rubbed off on her (Janet is now a highly competent fly fisher!)

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ABSTRACT

Morphometric analysis of Loch Rannoch charr indicated that in addition to the pelagic morph previously described, the benthic morph previously described consists of two distinct morphs. Thus one form had a relatively small head, short gill rakers and consumed only benthic invertebrates, whilst the other had a relatively large head and consumed benthic invertebrates until a size of 16cm at sizes above which it consumed other fish. These two forms were termed the benthivorous and piscivorous morphs respectively. Morphometric and dietary analysis agreed with the previous description of the third form (Walker *et al.*, 1988) as a pelagic planktivore which had fine head and jaw features, long gill rakers and a relatively streamlined morphology and differed from the other two morphs in that it was highly coloured as opposed to being cryptically coloured. This form was termed the planktivorous morph. Each morph was reproductively isolated by each spawning in a discrete location. Thus, the benthivorous morph spawned in the mouth of the largest afferent river, the River Gaur which enters the west basin of the loch, the piscivorous morph spawned in sublittoral regions of the east basin of the loch and the planktivorous morph spawned in shallow littoral regions throughout the loch but mainly in the east basin. Outwith the spawning period benthivorous and piscivorous charr were restricted to the west and east basins respectively indicating that each is adapted to the biotic conditions within each basin and that the basins have effectively isolated these two morphs.

Morphometric analysis of the charr of Loch Ericht a similarly sized lake within the same catchement as Loch Rannoch demonstrated the existence of two distinct morphs. One morph exhibited cryptic colouration and had a large head and was found to consume benthic invertebrates until a size of 16cm at sizes above which it consumed other fish. The other morph was highly coloured, had a relatively small head and streamlined body and consumed predominantly zooplankton. These forms were termed the piscivorous and planktivorous morphs respectively. There was some evidence that as with Loch Rannoch piscivorous and planktivorous charr, Loch Ericht charr were similarly reproductively isolated on the basis of depth of capture during the spawning period with planktivorous charr spawning in shallow littoral regions and piscivores spawning in deeper water.

Morphological analysis of the charr of Loch Tay, the third of the three largest lochs within the Tay catchement, indicated that these were monomorphic i.e. did not exhibit polymorphism and were planktivorous. However, a small percentage of fish were found to differ slightly in colouration, morphology and diet suggesting that some degree of trophic differentiation exists in Loch Tay charr.

Morphometric comparison of all six charr populations above indicated that L. Rannoch and Ericht piscivorous morphs were morphologically similar and differed from all other populations which were themselves similar to each other. In addition to this loch specific morphological traits separated Loch Rannoch charr from Loch Ericht and Tay charr. Loch Rannoch benthivorous charr were distinguished by having the shortest gill rakers of all six populations.

Differences in several life history traits were examined for planktivorous, benthivorous and piscivorous morphs of Arctic charr from Loch Rannoch. Piscivorous fish were the longest lived (maximum age of 17+ years) followed by benthivorous and planktivorous fish (11+ and 7+ respectively). Piscivorous females matured at 1+, as opposed to planktivorous and benthivorous females, which matured at either 2+ or 3+. Differences in length at age were detectable from an early age with piscivorous fish growing slowly but maintaining growth throughout their lifetimes. Planktivorous and benthivorous fish grew fast initially but reached an asymptote after 3+ years. The asymptotic size (L_∞) determined by the Von-Bertalanffy growth equation of planktivorous fish (216mm) was smaller than for benthivorous fish (238mm) which was in turn smaller than for piscivorous fish (404mm). Reproductive output in terms of both fecundity and egg mass was highest for benthivorous fish, followed by planktivorous then piscivorous individuals.

In all three lochs, brown trout and charr showed similar patterns of habitat and resource partitioning with brown trout utilising the littoral zone, planktivorous charr utilising sublittoral and pelagic zones and benthivorous and piscivorous charr utilising both the sublittoral and profundal zones. Planktivorous charr fed on zooplankton during the summer and switched to a benthic diet during the winter. Piscivorous and benthivorous charr consumed benthic invertebrates throughout the year although larger piscivorous individuals mainly consumed other fish. The parasite *Diphyllobothrium* sp. was present in charr throughout most size classes in planktivorous charr, this was therefore attributable to transmission by ingestion of copepods which are the intermediate host of this parasite. Trout and piscivorous charr which did not depend on zooplankton as a food resource exhibited infection only at sizes above which they became piscivorous indicating that their infection with *Diphyllobothrium* was a result of ingesting fish already infected with the parasite (paratenic transmission). Benthivorous fish were seldom infected with this parasite. The acanthocephalan parasite *Echinorhynchus truttae* was found in high numbers in all brown trout populations and seldom found in charr. Given that these parasite is transmitted by ingestion of its intermediate host *Gammarus* sp. and that *Gammarus* is found epibenthically in littoral areas, the high levels of infection of this species in trout reflect their habitat and dietary utilisation.

A particular threat to the ecology of Loch Rannoch and its charr community was identified when a crucian carp was caught in the Loch. Establishment of an alien species such as this in Loch Rannoch is likely to result in increased levels of competition for resources with potentially detrimental effects for the charr community.

CHAPTER 1 - GENERAL INTRODUCTION

1.1 Systematics and biogeography of Arctic charr

Arctic charr *Salvelinus alpinus* is one of six species of the *Salvelinus* genus, the other five species being the Dolly varden charr *Salvelinus malma*, the brook charr *Salvelinus fontinalis*, the lake trout *Salvelinus namaycush*, the Japanese charr *Salvelinus leucomaenis* and the bull trout *Salvelinus confluentus* (Phillips *et al.*, 1994). Their phylogenetic relationship with other salmonid fish can be seen in Fig. 1.1 and their relationships with each other in Fig. 1.2. Lake trout, brook charr and bull trout are confined to north America, Dolly varden to the land regions bordering the Northern Pacific and Japanese charr to east Asia (Behnke, 1972; Phillips *et al.*, 1994). Arctic charr, although overlapping with Dolly Varden charr to some extent, is the most northerly occuring member of the *Salvelinus* genus and indeed all freshwater fish species. It is present in Arctic and sub Arctic land regions e.g. Scandinavia, Iceland, Greenland, Alaska, Siberia and numerous Arctic islands (Johnson, 1980). The species' occurrence at low latitudes is facilitated only by the presence of large, deep lakes which do not attain critically high temperatures during the summer or by existing at higher altitudes (Machino, 1991), as is the case with Alpine populations which represent the southerly limit of the species.

As with other salmonid species, e.g. brown trout (*Salmo trutta*; Elliott, 1994) sockeye salmon *Oncorhynchus nerka*; (Burgner, 1991; Wood and Foote, 1996) and Rainbow trout (*Oncorhynchus mykiss*; Hart, 1973), Arctic charr also exhibit

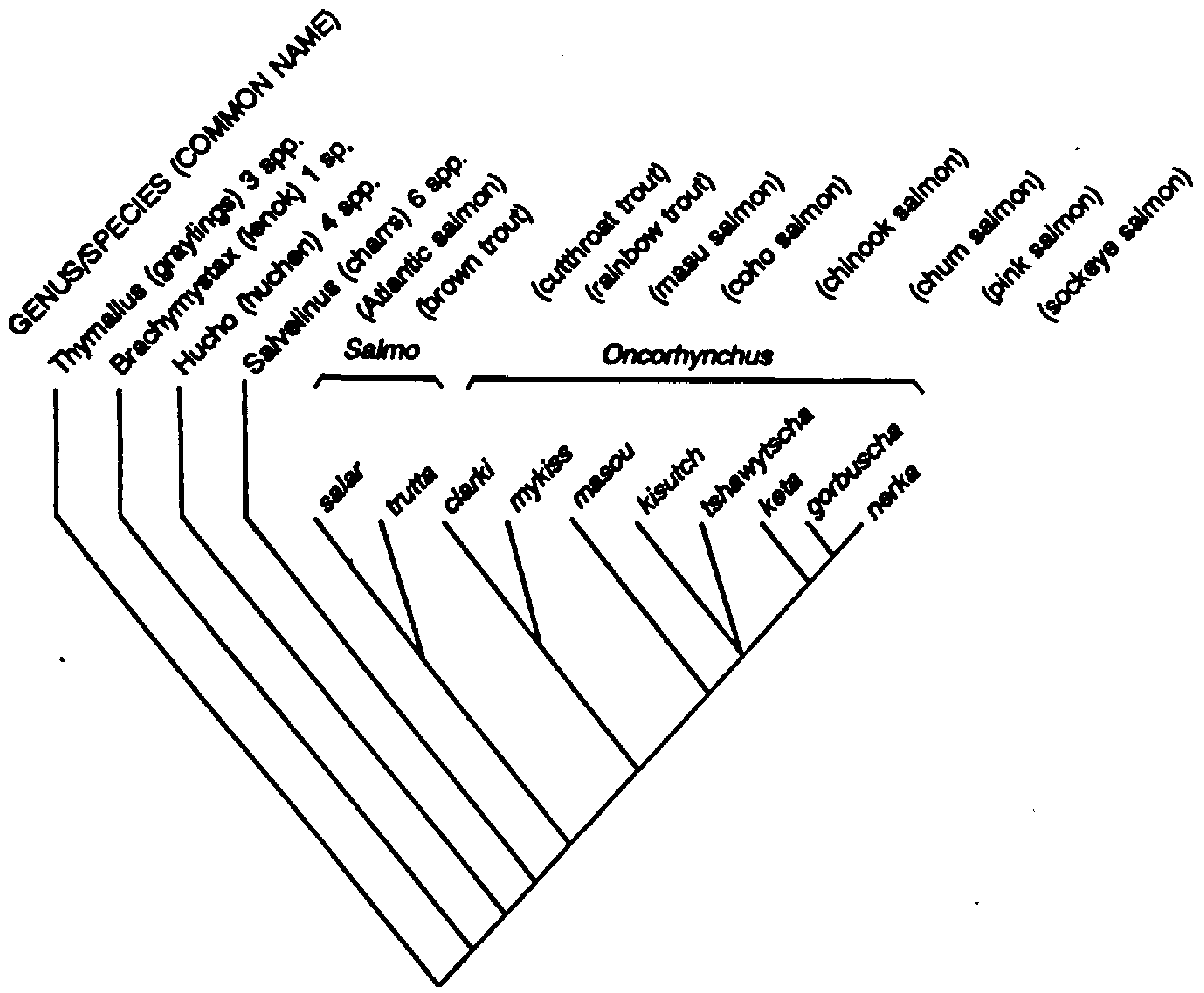

Figure 1.1 Phylogenetic relationships of the salmonids (taken from Elliott (1994) after Smith and Stearley (1989).

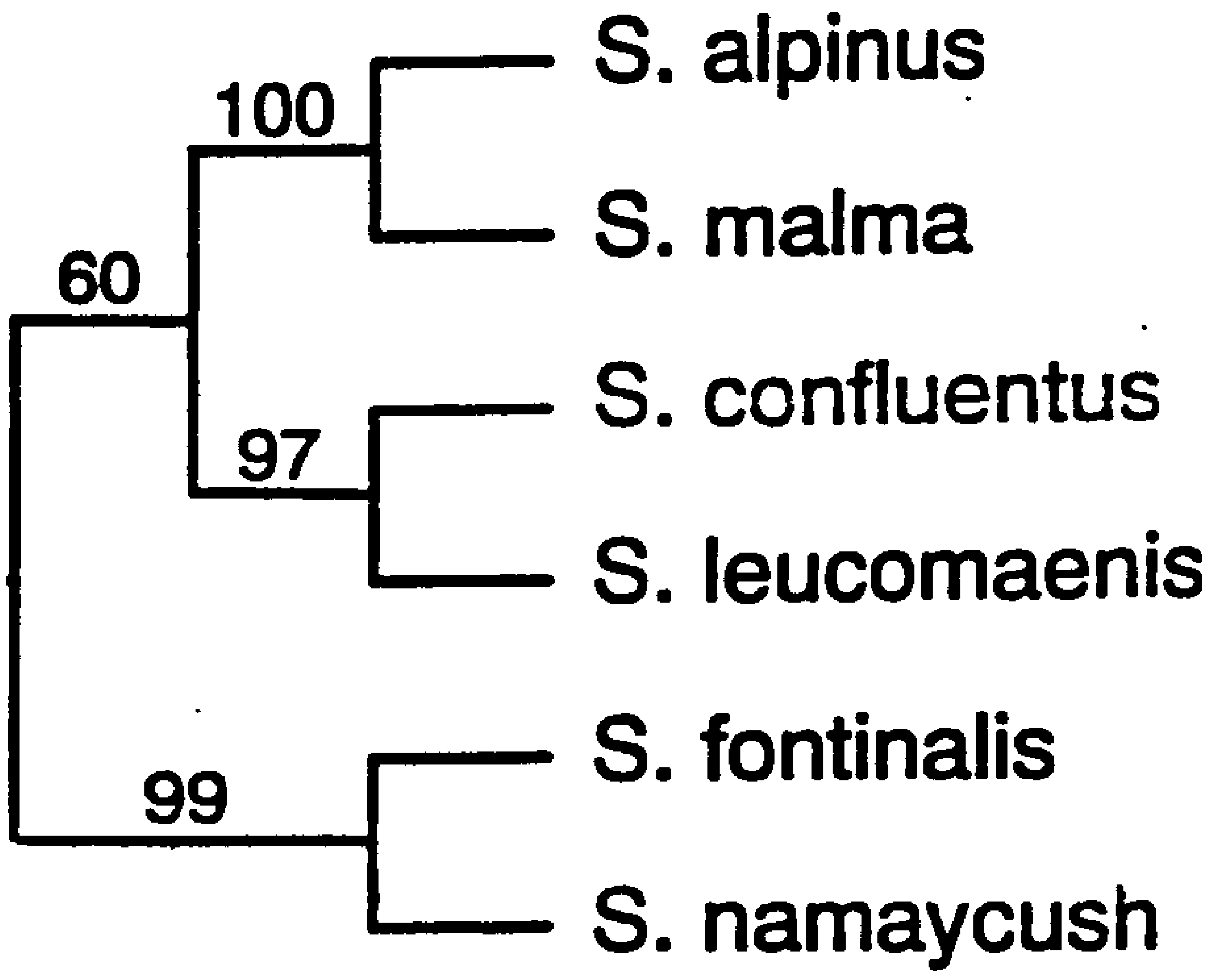

Figure 1.2 Phylogenetic relationships of species of the genus Salvelinus. Numbers indicate bootstrap values. (Taken from Phillips *et al.*, 1993).

both freshwater resident and sea migratory or anadromous forms (Johnson, 1980). The degree to which anadromy occurs is strongly affected by latitude, frequency of anadromy increasing with latitude and all populations south of approximately 65° N being entirely freshwater resident despite many having direct access to the sea (Johnson, 1980).

One of the most striking features of the species is its considerable variability in terms of its appearance. This diversity is manifest most clearly in freshwater resident populations due to genetic isolation and adaptation to specific water bodies which provide relatively heterogeneous habitats. Anadromous populations, although differing from other freshwater resident populations tend to be similar in appearance to each other, due to the marine environment being a relatively homogenous habitat therefore promoting reduced variability in morphology, at least during the marine phase (Nicieza, 1995).

1.2 Sympatric polymorphisms in freshwater fish

A number of freshwater fish species exhibit two or more discrete forms or morphotypes (morphs) within a single lake which differ noticeably in appearance. Such variation usually has a trophic basis and is therefore known as trophic polymorphism (Robinson and Wilson, 1994; Smith and Skúlason, 1996). Typically such polymorphisms consist of a benthivorous and a planktivorous feeding morph, each of which has a distinctive morphology adapted to the habitat which it utilises and the prey which it consumes. McPhail (1984) demonstrated that benthic feeding and limnetic feeding forms of *Gasterosteus* sp. occurred in

Lake Enos, Vancouver Island. The limnetic form had significantly higher numbers of longer gillrakers, shallower bodies and longer heads than the benthic form. Similarly Robinson *et al.*, (1993) describe the occurrence of two forms of pumpkinseed sunfish *Lepomis gibbosus* in certain lakes. As well as the typical shallow-water snail eating form, an open-water planktivorous form was found to exist which had longer, more numerous gill rakers and a shallower body. Similarly, sympatric benthic and pelagic feeding morphs of whitefish (*Coregonus* and *Prosopium* sp.) are widespread and have been recorded from Scandinavia and North America (Lindsey, 1981).

In extreme cases, lakes may contain numerous sympatric morphs of a single species. Such communities are commonly referred to as species flocks (e.g. Nagelkerke *et al.*, 1994). The cichlids of the African Great Lakes (Lakes Victoria, Tanganyika and Malawi) represent the best known example of this phenomenon. Aproximately 500 cichlid species are known to exist in Lake Victoria (Galis, 1998) which exhibit extremely diverse trophic adaptations (see Liem, 1991; Yamaoka, 1991). Nagelkerke *et al.* (1994) and Nagelkerke *et al.* (1995) determined that 14 morphs of barb *Barbus intermedius* occurred in Lake Tana, Ethiopia. The morphs exhibited a variety of morphologies each corresponding to a specialised feeding niche which included piscivory, benthivory, planktivory, detritivory and herbivory.

1.3 Sympatric polymorphism in Arctic charr

Amongst temperate freshwater fish the Arctic charr is the species that exhibits polymorphism most frequently, the most notable example of this being the four morphs present in Thingvallavatn, Iceland (Sandlund *et al.*, 1992). The four morphs are: a small benthivore which occupies the interstitial spaces within the lava substrate of the lake and feeds predominantly on gastropods, a large benthivore which lives epibenthically and also feeds on gastropods, a planktivore which occupies the pelagic zone and feeds on zooplankton and a piscivorous form which lives pelagically and feeds predominantly on threespined sticklebacks *Gasterosteus aculeatus* once a critical length of 22cm is reached (Sandlund *et al.*, 1992). The more common situation is of two morphs co-occurring in a single lake. This has most frequently been reported from Scandinavian countries where typically a smaller, often referred to as "Dwarf" benthic morph (so called due to its maturation at small size, small asymptotic size and benthic macro-invertebrate diet) co-exists with a so called "Normal" pelagic morph (which matures at a larger size, reaches a larger asymptotic size and feeds predominantly on zooplankton, (Nilsson and Filipsson, 1971; Klemetsen and Grotnes, 1975; Hindar and Jonnson, 1982; Nordeng, 1983; Svedäng, 1990; Parker and Johnson, 1991)).

Charr, as with other freshwater fish species, most noticeably threspined sticklebacks (Schluter and McPhail, 1993) show remarkable parallelism in trophic morphology amongst morph pairs. Thus, planktivorous morphs of all species tend to show similar adaptations, having shallower, streamlined bodies, with small heads, features which enable sustained swimming (Swain and Holtby, 1989;

Taylor and Foote, 1991). Fine jaws and numerous, long gill rakers are also features of planktivorous morphs (e.g. Schluter and McPhail 1993) which enable effective capture and retention of zooplankton (Hessen *et al.*, 1988). Dwarf or benthivorous charr morphs tend to have larger heads with larger, more robust jaws (Gardner *et al.*,1988) and fewer, shorter gill rakers (Lindsay, 1981). The morphologies of planktivorous charr morphs are thus similar to those described for anadromous forms (Johnson, 1980) as both occupy essentially open water pelagic habitats. Thingvallavatn charr demonstrate adaptive morphology in a manner unique amongst documented polymorphic populations. Both benthivorous morphs have substantially shortened bottom jaws (Sandlund *et al.*, 1992) an adaptation enabling them to efficiently remove benthic prey items such as the snail *Limnaea pereger* which is their predominant prey item (Snorrason *et al.*, 1989). Conversely terminal mouths in the planktivorous and piscivorous morphs are typical of fish which snap food particles (Keast and Webb, 1966).

Anadromous charr as with other anadromous salmonids adopt a predominantly silver colouration during their marine phase. Freshwater resident individuals from anadromous populations often posses dull colouration and retain parr marks even when mature. Corresponding adaptations have also been recorded in pelagic planktivorous morphs which exhibit colouration corresponding to anadromous individuals and dwarf benthic morphs which exhibit colouration corresponding to stream resident individuals (Jonnson and Hindar, 1982; Svedäng, 1990; Parker and Johnson, 1991; see Fig. 5 in Sandlund *et al.*, 1992). Thus silver colouration appears to be an adaptation to a pelagic habitat. Pelagic morphs also frequently exhibit reddening of the ventral surface, this being due to carotenoid pigments derived from zooplankton (Hatlen, 1997). Such reddening may be intensified in males during the spawning period (Johnson, 1980) which together with prominent whitening of the leading edges of the fins (see Fig. 27 in Sandlund *et al.*, 1992) represent male secondary sexual characteristics. No secondary sexual characteristics occur in females or in benthic morphs (Hindar and Jonsson, 1982; Sandlund *et al.*, 1992).

1.4 Polymorphic charr in the British Isles

In the British Isles over 200 populations of charr are known to exist, the majority of these being in Scotland and to a lesser extent Ireland. All eight English populations occur in the Cumbrian Lake District and five populations are known to exist in Wales (Maitland and Lyle, 1991). Due to the southerly latitude of the British Isles, all populations are entirely freshwater resident. Generally, British charr have been less extensively studied than in other countries although they have been the subject of some scientific investigation for example by Barbour (1984), Partington and Mills (1988), Maitland (1991) and Baroudy (1994). The charr of Lake Windermere, Cumbria represent the most studied charr population in the UK. Lake Windermere charr are unique because they comprise four populations, consisting of discrete north basin and south basin populations each of which are further comprised of spring and autumn spawning populations (Partington and Mills, 1988). While temporal differences in spawning between morphs or populations are not unique (e.g. Jonsson and Hindar, 1982; Skúlason *et al.*, 1989) the fact that there is no trophic and very little morphometric basis for population segregation is unique. However, clear differences existed in gill raker lengths and numbers between spring and autumn spawners and tagging recaptures show fish returning to the same spawning site annually (Kipling and Le Cren, 1984). Furthermore, significant electrophoretic differences between basin populations (Partington and Mills, 1988) demonstrate that these populations are genetically discrete.

Only one instance of true trophic polymorphism in the British Isles has been documented. Walker *et al.* (1988) and Gardner *et al.* (1988) describe the occurrence of a benthic and a pelagic morph in Loch Rannoch in Perthshire, Scotland. The pelagic form was typical of pelagic or normal charr described elsewhere in that it had a smaller head, finer jaws, longer, finer gill rakers and greater colouration than the benthivorous morph. The benthivorous morph while displaying dull colouration and parr marks as has been observed with benthic dwarf morphs did not exhibit dwarf growth characteristics and indeed individuals of this morph were amongst the largest of all charr captured. Differences in diet were also found with the pelagic form almost exclusively consuming zooplankton and the benthic form consuming benthic invertebrates. However, subsequent non-systematic observations of the L. Rannoch charr suggested that the situation may be more complex than had been described and that more than two morphs possibly existed.

1.5 Life history characteristics of Arctic charr

As with morphology and ecology, life history variables differ greatly amongst charr populations (Johnson, 1980). The largest differences are observed between anadromous and freshwater resident forms with anadromous forms having significantly higher age at maturity, fecundity and longevity (Tallman *et al.*, 1996) and spawning relatively infrequently by being reproductively dormant in some years (Dutil, 1984; 1986).

Amongst freshwater resident populations age and size at maturation are also extremely variable. In a review of studies of 40 freshwater resident populations Tallman *et al.* (1996) found the lowest observed age at maturation to be 2 years (Martin, 1955), the highest was 11 years (Johnson, 1983) the mean age at maturity being 4.5 years. In a similar study, Vøllestad and L'Abée-Lund (1994) found the smallest size at maturation to be 92mm in dwarf benthivorous charr from Thingvallavatn with the largest at 409mm in charr from LacNoname, Canada (Fraser and Power, 1984).

The factors governing the maturation process have been examined by rearing experiments. Thus, Svedäng (1990) determined that Stora Rösjön dwarf charr matured earlier and at a smaller size than normal charr in the wild and in captivity when reared under identical conditions although each morph matured earlier in captivity than they did in the wild due to faster growth rates in captivity. Similarly, Skúlason *et al.* (1996) observed discrete growth rates and ages of maturation in progeny of the four morphs of charr from Thingvallavatn reared under identical conditions with the small benthivorous and planktivorous morphs maturing in their second and third years whereas no large benthivorous charr matured during this time. As with the study of Svedäng (1990) planktivorous charr matured earlier in captivity than in the wild, again presumably due to better growing conditions in captivity. Male charr were found to mature earlier than females in these studies, a phenomenon widely, reported in salmonids (Alm, 1959; Bagliniere and Maisse, 1985; Gross, 1985; Thorpe, 1986; Elliott, 1994; Cavalli and Chappaz, 1996). It can therefore be seen that growth and age at maturity are both genetically and environmentally determined.

In populations in which polymorphisms appear to be the consequence of different developmental routes the principal mechanism determining whether a fish adopts a strategy to mature as a dwarf or to delay maturity and mature as a normal appears to be growth rate at an early developmental stage (Hindar and Jonsson, 1993). In a study of four lakes on Northern Ellesmere Island, each containing dwarf and normal individuals, Parker and Johnson (1991) found that the lakes which had the fastest growing charr during their early life stages had the highest proportion of normal charr. In contrast, in the Atlantic salmon *Salmo salar,* parr which exhibit the fastest growth rates mature earliest, as parr (essentially dwarf salmon), and do not undertake a seaward migration prior to maturation, a process known as precocious maturation (Bagliniere and Maisse, 1985).

As with *Salmo* sp., individuals of *Salvelinus* genus are capable of repeat spawning (iteroparity). In more northerly charr populations, harsh climatic conditions may limit growth opportunities. This has the result of reducing spawning frequency as fish can not obtain enough energy in a single years feeding to replenish energy lost through spawning (Dutil, 1986). In less severe climatic regions such as the British Isles some freshwater resident charr populations may spawn in consecutive years after maturation (Barbour, 1984; Kipling and Le Cren, 1984).

Arctic charr have small eggs compared to other salmonids. Wallace and Aasjord (1984) recorded mean egg diameters of 4.2mm in Arctic charr, 5.1mm in rainbow trout, *Oncorhynchus mykiss*, 5.2mm in brown trout, *Salmo trutta,* 6.2mm in Atlantic salmon and 7.5mm in pink salmon, *Oncorhynchus gorbuscha.* Egg size is however highly variable in charr and ranges from 3.6mm-5.0mm (Johnson, 1980). Fecundity is widely reported to increase with body size in a variety of fish species including salmonids (e.g. Bagenal (1969a) on brown trout; Thorpe *et al.* (1984) on Atlantic salmon; Jonsson *et al.*(1988) on Arctic charr). This relationship may be complicated by the fact that egg size also increases with body size. Egg size has implications for the future survival of offspring because larger eggs result in larger alevins (e.g. Thorpe *et al.*, 1984) which in turn have higher survival rates (Bagenal, 1969b). Baroudy and Elliott (1994) thus attributed the fact that only a small proportion of the Lake Windermere charr population consisted of spring spawners to the significantly smaller egg sizes of spring spawners which they experimentally demonstrated had lower survival rates than the autumn spawners.

1.6 Genetic basis of Arctic charr polymorphisms

One fundamental question is: do sympatric morphs represent isolated breeding populations (gene pools) or are they merely consequences of different developmental routes of a single genotype resulting from different feeding opportunities in differing habitats?

There appears to be evidence for both situations existing. Nordeng (1983) demonstrated by rearing and transplantation experiments that resident "dwarf", resident "normal" and anadromous charr in Norway could each be obtained from any of the parental morphs, thus demonstrating that these forms were consequences of different developmental routes. Hindar and Jonsson (1993) demonstrated by similar means that the "dwarf" and "normal" charr from Lake Vansgvatnet, Western Norway were derived from a single parr morphotype. However, the large degree of assortative mating observed in the field (Jonsson and Hindar, 1982) and a tendency for parental growth rate and jaw morphology to be inherited under identical rearing conditions indicated that there was some genetic component involved in maintaining this polymorphism. Riget *et al.* (1986) describe a trimodal length frequency distribution in the charr of Lake Taseruaq, Greenland. Charr of the three groups were segregated on the basis of both diet and habitat. The smallest individuals occupied the profundal zone down to 50m depth and fed mainly on chironomids, the medium sized charr occupied the pelagic zone and fed mainly on zooplankton when abundant and the largest individuals occupied all regions of the lake and were primarily cannibalistic. Genetic analysis of these morphs indicated that they represent a single genotype. Furthermore fish were able to transfer from one group to another by a period of rapid somatic growth by suppressing maturation. A similar situation was described by Klemetsen *et al.* (1985) on Bear Island in the Barents sea where charr in three out of five systems examined showed a bimodal length frequency distribution. The small and large modes appeared to be partially segregated on the basis of habitat and diet as well as morphology and appearance with small mode charr exhibiting a similar appearance to "dwarf" charr described elsewhere. Despite these differences, the fact that the two modes in each of the two morph (mode) configurations had no genetic differences, based on esterase analysis, suggests that again they are consequences of different developmental routes which possibly have some genetic components, as significant differences in pyloric cecae and gill raker counts and head morphology were recorded. However although no direct evidence was found for individual fish transferring from one mode to another, the fact that no small large-mode fish were identified indicates that this was probable. Such phenotypic plasticity, allowing a single fish to change morphs, was also apparent in the experiments of Nordeng (1983) and Hindar and Jonsson (1993) described previously. A single fish may thus exist as all three morphs within a lifetime by means of such ontogenetic shifts.

In contrast to the above situations there are several instances of polymorphism in which good evidence has been provided for each morph being a reproductively isolated spawning population. Skúlason *et al.* (1989) demonstrated that parental morphologies of Thingvallavatn charr were inherited under identical rearing conditions, although few morphological differences were found between offspring of the piscivorous and planktivorous morphs, indicating that these two morphs are consequences of ontogenetic shifts and belong to the same gene pool.

Rearing experiments of dwarf and normal charr from Stora Rösjön in Sweden by Svedäng (1990) determined that parental dwarf charr matured as dwarfs whereas parental normal charr matured as normals indicating that these morphs are genetically based rather than a consequence of developmental routes.

1.7 Mechanisms maintaining reproductive isolation in polymorphic fish communities

One of the principal factors promoting population divergence in salmonids is the strong tendency for fish to accurately return to their natal stream or area of lake to spawn (Hastler, 1954, 1956; Horrall, 1981). If spawning sites are non-continuous this will result in restricted gene flow between adjacent spawning groups. Of the three morphs of brown trout in Lough Melvin, Ferguson and Taggart (1991) recorded that one spawns in shallow bays and in the mouth of the efferent river, one spawns in smaller afferent rivers and the upper reaches of the main afferent river while the third spawns in the deeper parts of the lower reaches of the same river. Similar homing behaviour and reproductive isolation was seen in the barbs of Lake Tana, Ethiopia by Nagelkerke *et al.* (1996), with morphs spawning in four different afferent rivers and at different locations within the rivers and two morphs spawning in the lake itself. This segregation was further reinforced by differences in spawning time among morphs. In lacustrine charr morphs, spatial segregation has been reported on the basis of depth of spawning sites for dwarf and normal charr in Lakes Vangsvatnet (Jonsson and Hindar, 1982) and Svirdalsvatn (Hesthagen *et al.*, 1995), Norway. In each case, dwarf charr were found to spawn at greater depths than normal charr. In the case of Lake Svirdalsvatn isolation was reinforced by dwarf charr spawning in July to September and Normal charr spawning entirely in November. Temporal segregation was less pronounced in Lake Vangsvatnet with a large degree of overlap but different peaks of spawning time.

Where no temporal or spatial segregation in spawning exists between morphs, behavioural interactions between individuals of different morphs may play a role in maintaining some degree of reproductive isolation. For example, Svedang (1992) demonstrated that when dwarf and normal charr were spawning in the same place at the same time, male dwarf charr mated with normal females by employing a sneaking tactic although dwarf males experienced a higher degree of aggression than normal males from normal females. Size assortative mating is known to occur in salmonids (e.g. Kitano, 1996) and is likely to play a role in isolating small benthivorous, planktivorous and larger piscivorous charr in Thingvallavatn (Sigurjonsdottir and Gunnarsson, 1989) which overlap in spawning time within the ranges of September to November, with the large benthivorous morph being temporally isolated, spawning in late July and August over coldwater springs (Skúlason *et al.*, 1989).

1.8 Speciation processes in polymorphic salmonid communities

Another fundamental question regarding the existence of such polymorphic charr populations is: do the observed morphotypes exist as a result of evolutionary processes which have occurred within the lake which they currently inhabit (sympatric processes) or do they represent populations which have evolved prior to or during the last ice age in separate glacial refuges (allopatric processes) and have subsequently invaded a common habitat? This question is important as it addresses the timescale over which charr forms have evolved, as sympatric processes necessitate morph formation within, at most, 10 000 years.

This question has principally been addressed by the use of molecular genetic techniques. Nyman (1972) and Nyman *et al.* (1981) proposed on the basis of the frequency of the Est^F allele and loosely correlated ecological data from Swedish, Norwegian and Canadian charr populations that three allopatrically derived sibling species of Arctic charr existed that had subsequently, in post glacial times introgressed to varying degrees resulting in the large degree of variability in forms now present.

More recently, an electrophoretic study of charr from fifteen Norwegian Lakes (Hindar *et al.*, 1986) found no evidence for sibling species as all populations were genetically similar. Analysis of three polymorphic populations consisting of dwarf and normal charr and one population with co-occurring resident and anadromous fish indicated that there were more similarities between sympatric "normal" and "dwarf" charr from any one lake than there were between normal or dwarf charr from different lakes. Similarly anadromous and resident charr from the same locality were genetically similar in relation to amongst locality comparisons.

The above studies, together with studies by Ferguson (1981), Magnusson and Ferguson (1987) and Partington and Mills (1988), detected very little variation in Arctic charr at the electrophoretic level. More recent studies have therefore focused on mitochondrial DNA (mtDNA) analysis. Based on mtDNA Danzmann *et al.* (1991) proposed that the close genetic similarities among the Thingvallavatn charr morphs indicated that they had evolved recently from a common ancestor, strongly suggesting sympatric divergence.

Further evidence against the allopatric speciation hypothesis is provided by analysis of minisatellite and mtDNA of kokanee (freshwater resident) and co-occuring anadromous morphs of *O. nerka* which co-occured in a variety of locations bordering the North Pacific Ocean (Taylor *et al.*, 1996). As with the study of Hindar *et al.* (1986) on charr, it was found that closer genetic similarities existed between co-occuring Kokanee and sockeye than amongst any one morph from different localities. It should be noted that in each of the latter two studies, evidence for two allopatrically derived invading groups was also found although these groups now largely occur in different geographic regions and are in no way responsible for the polymorphic populations thus described. In a study of seven populations of lake whitefish, *Coregonus clupeaformis* in eastern North America, each of which consisted of a dwarf and normal morph, Pigeon *et al.* (1997) proposed on the basis of mtDNA that morphs had arisen by sympatric evolution although there was also evidence for allopatric separation and secondary contact in some lakes.

Despite the widespread occurrence of polymorphism in Arctic charr, the occurrence of trophically and morphologically discrete brown trout has only been documented from a single water body. Ferguson and his co-workers (Ferguson and Mason, 1981; Ferguson and Taggart, 1991) describe the presence of three discrete morphs of brown trout from Lough Melvin, Ireland, a planktonic (sonaghen), a benthivorous (gilaroo) and a piscivorous (ferox) morph. Analysis of allozymes suggested that the ferox morph resulted from a single postglacial invasion and that the sonaghen and gilaroo were sympatrically derived from a common invading ancestor. More recently however, studies using mtDNA by Hynes *et al.* (1996) suggest that the three forms represent three allopatrically derived stocks.

Amongst the strongest evidence for sympatric processes being responsible for polymorphims comes from instances where transpantations of a single morph are made to a water body not previously containing that species, whereafter both morphs come to exist in that water body. Thus, introductions of anadromous sockeye salmon *Oncorhynchus nerka* to systems in New Zealand with access to the sea which did not previously contain the species, resulted in the establishment of freshwater resident kokanee (Scott, 1984). Similarly, transplantation of fry of normal charr from Lake Tinnsjøen to a catchment not previously containing charr resulted in the establishment of both dwarf and normal charr within that system (Hindar *et al.*, 1986).

1.9 Insights into speciation processes from studies of threespined sticklebacks

The most extensively studied polymorphic sympatric fish populations are those occurring in a series of lakes in coastal British Columbia (McPhail, 1994). Experimental studies of these populations has provided strong evidence that morphological divergence of trophic traits and hence the existence of two distinct morphotypes has resulted from intraspecific competition within a monomorphic ancestral form. Thus Schluter (1994) compared the growth of monomorphic threespined sticklebacks exhibiting a range of trophic morphologies in the presence and absence of sticklebacks exhibiting limnetic morphology. In the absence of limnetics, all fish grew equally well irrespective of morphology. In the presence of limnetics, however, faster growth was exhibited by individuals which were most morphologically different from the limnetics, as there was less competition for the prey which they could most efficiently consume, and poorer growth was exhibited by fish which exhibited similar morphologies to the limnetics due to increased competition for prey items which such fish could most efficiently utilise.

1.10 Aims

Given the possibility of a third charr morph in L. Rannoch and speculation that other polymorphic charr populations may exist in Scottish lochs (Walker *et al.*, 1988), L. Rannoch and the two similarly sized lochs, L. Ericht and L. Tay, occurring within the same catchment (Fig. 1.3), provide ideal locations in which to investigate charr polymorphism further. It is the charr populations of these three lochs therefore, that are the basis of this study.

This thesis aims to answer the following questions:

1) Does the benthic morph described by Walker *et al.* (1988) consist of two distinct morphs? If so what is the basis of this segregation? (chapter 2)

2) How do the morphs differ in terms of population structure and life history strategies? (chapter 5)

3) Do the charr of Loch Ericht and Tay exhibit polymorphism? If so, what is its basis? (chapter 3, chapter 4)

4) How do the charr populations in the three lochs examined compare morphometrically and do populations from different lochs which occupy similar trophic niches have similar morphologies? (chapter 4)

5) How are the charr morphs and brown trout segregated in the three lochs investigated in terms of habitat utilisation, diet and patterns of parasite infection? (chapter 6)

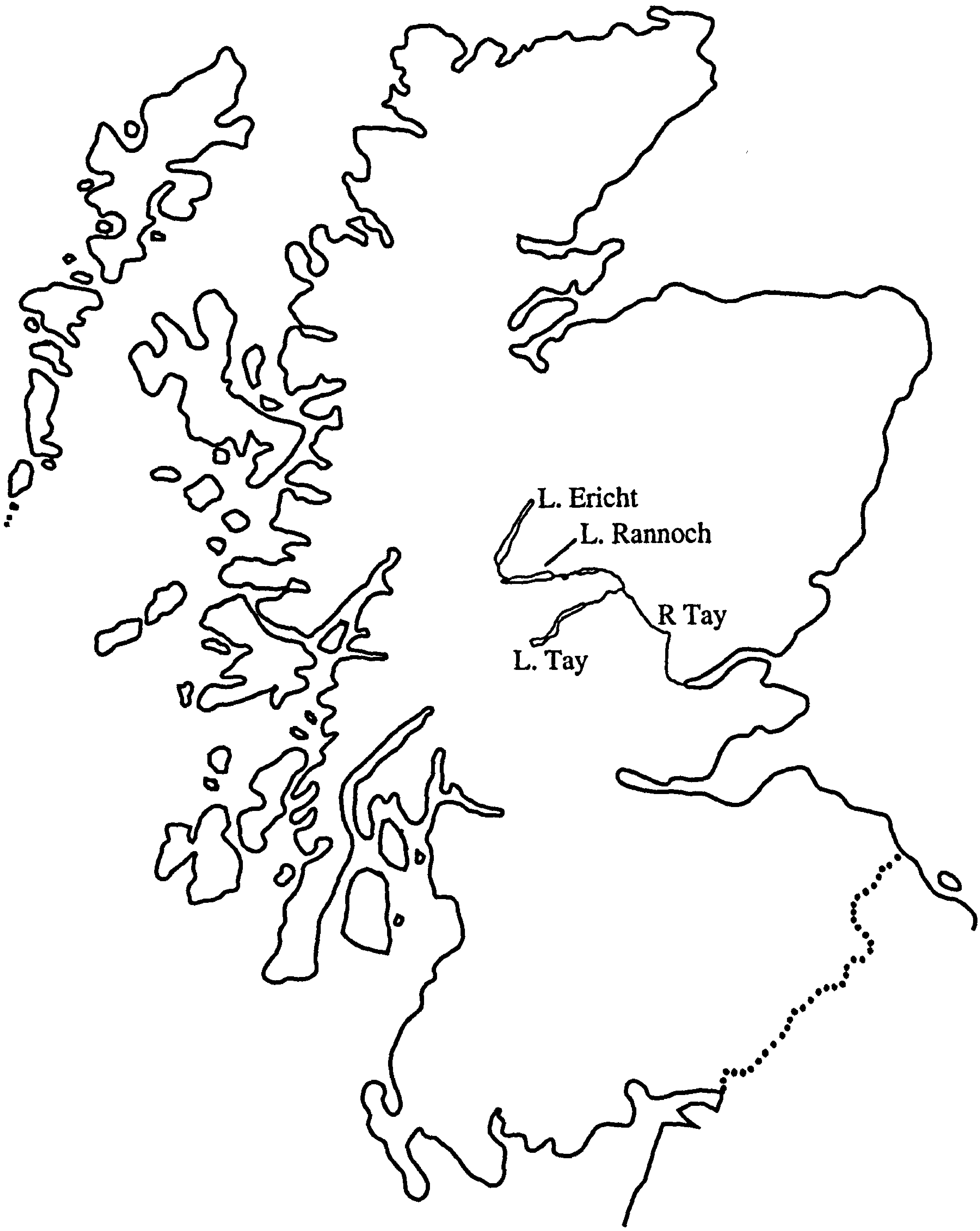

Fig. 1.3 Locations of the three study lochs.

[1]CHAPTER 2 - TROPHIC POLYMORPHISM IN THE ARCTIC CHARR OF LOCH RANNOCH

2.1 Introduction

Phenotypic variation between populations of the same species is common in fishes, particularly freshwater forms. Such variation has been interpreted typically as being the result of local evolutionary pressures acting upon a common ancestral form in different ways and is often seen as one step towards full speciation (Skulason and Smith, 1995). The occurrence of such polymorphism is particularly common in certain taxonomic groups, the salmonids for example (Taylor, 1991), resulting in part from differences in the degree to which species have retained phenotypic flexibility (Day *et al.*, 1994; Skulason and Smith, 1995). Among the salmonids the Arctic charr *Salvelinus alpinus* (L.) exhibits the greatest extremes of phenotypic variability, in the form of between population variability in body shape, in colour and in behaviour. Additionally in this species it is not uncommon to find disjunction of phenotypic variability within a single water body in the form of morphologically distinct types living in sympatry (e.g. Klemetsen and Grotnes, 1980; Hindar and Jonsson, 1982; Klemetsen *et al.*, 1985; Snorrason *et al.*, 1994).

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[1] This chapter is the basis of a paper: Adams, C. E., Fraser, D., Huntingford, F. A., Greer, R., Askew, C. M. & Walker, A. 1998. Trophic polymorphism amongst Arctic charr from Loch Rannoch, Scotland. *Journal of Fish Biology* **52**, 1259-1271.

In Scotland, only one polymorphic population of Arctic charr has been described to date. Walker *et al.*, 1988 and Gardner *et al.*, 1988 described 2 distinct morphs from Loch Rannoch, Perthshire, differing in colouration, body shape, head size and diet. One morph, the pelagic morph, is streamlined in shape, brightly coloured (and sexually dimorphic in this respect) and feeds on pelagic zooplankton. The benthic form is deep bodied and less streamlined, cryptically coloured (with no sexual dimorphism) and feeds on benthic macro-invertebrates. During collections of these two forms of Arctic charr in the breeding seasons, two discrete spawning aggregations of the cryptically coloured charr were found at different parts of Loch Rannoch (Fig. 2.1). Non systematic observation suggested that, although the fish at the two sites were both cryptic, they might be distinct with regard to the morphology of their head and body, those collected from the River Gaur having smaller heads and being more streamlined (Fig. 2.2). In this paper, we present the results of a quantitative examination of the hypothesis that the fish spawning at the two sites represent distinct forms differing in morphology and ecology.

2.2 Materials and methods

Study site

Loch Rannoch (GR. NN5957 56°41.3' 4°17.7'W42) is situated in Perthshire, Scotland (Fig 1.3) at an altitude of 203m above sea level. It is a deep, oligotrophic fjiord-like lake, with a maximum depth of 116m (Murray and Pullar, 1910) and a mean depth of 51m. In addition to Arctic charr, the loch also contains brown trout, pike *Esox lucius* L., perch *Perca fluviatilis,* minnow *Phoxinus phoxinus* (L.), eel *Anguilla anguilla* (L.) Atlantic salmon and three-spined stickleback. All species

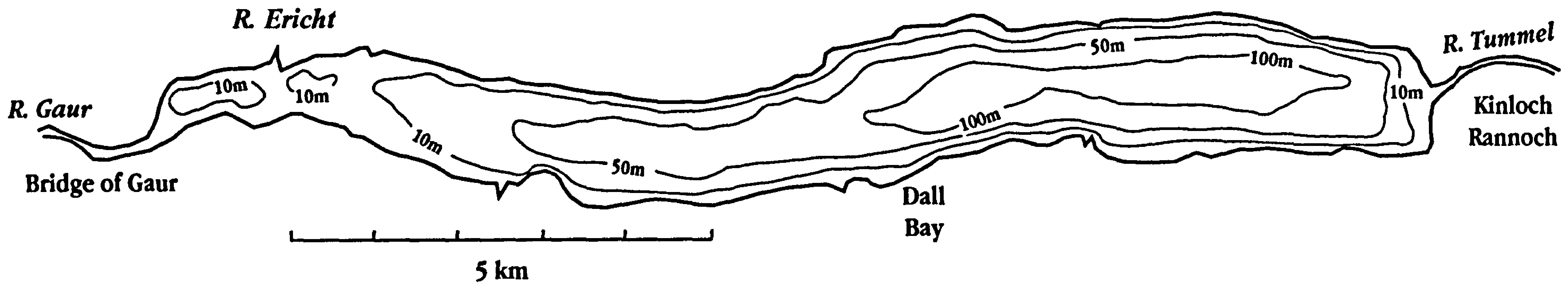

Figure 2.1 Loch Rannoch showing the collection sites at Dall Bay and the River Gaur.

Fig. 2.2 TOP PLATE: Three charr morphs from L. Rannoch: top fish = cryptically coloured Dall spawning (piscivorous) charr, middle fish = cryptically coloured R. Gaur spawning (benthivorous) charr, bottom fish = highly coloured (planktivorous) charr.

BOTTOM PLATE: Spawning charr present at Dall Bay region: Top three fish = cryptically coloured Dall spawning (piscivorous) charr, bottom three fish = highly coloured (planktivorous) charr.

other than brown trout and Arctic charr are either localised within the loch or very scarce (chapter 6).

Morphological characterisation of the morphs

During September and October 1992, charr were collected from Dall bay on the south shore of L. Rannoch (Fig. 2.1), (a known spawning site of the streamlined, brightly coloured pelagic morph) using multi-panel gill nets (nets 8-50mm bar mesh size) set in 1-10m water depth. The fish caught in these nets were mainly brightly coloured charr, but a small number of cryptically coloured fish (mostly ripe males and females that were ovulating or close to ovulation) were caught also. During October and November 1992, fyke traps (hoop size 50cm) were set in the lower reaches of the River Gaur (Fig. 2.1) in 1-3m depth, to intercept fish entering the river to spawn. These traps caught only cryptically coloured charr (all ripe), some brown trout *Salmo trutta* L. and an occasional perch *Perca fluviatilis* L. Fish were killed at the collection site and frozen within 6h.

To look for discontinuity in head morphology between cryptically coloured charr from the two sites, measurements of 11 morphometric characteristics were made on 30 fish in each category. In addition, for comparison, 30 brightly coloured charr from Dall Bay were subjected to the same procedure. Each fish was ascribed *a priori* to one of the three groups based firstly on colouration, separating brightly coloured from cryptically coloured charr, and then on spawning site, separating those caught at the mouth of the River Gaur from those captured at Dall Bay.

After defrosting, each fish was weighed (± 0.1g), measured (fork-length, ± 1mm) and photographed to give a close up lateral view of the head (tip of snout to the end of the pectoral fins) and a close up ventral view of the head, each with a suitable scale. The photographs were enlarged by 50% at printing and a series of head measurements made using a computerised digitising pad (Fig. 2.3).

Head characteristics were compared using multi and univariate techniques. The two indices of snout curvature were uncorrelated with fork length and so were compared between the two cryptic forms using univariate analysis of variance. The remaining characters increased with fork length, so were compared across the three categories of fish using univariate covariance analysis of character on fork length (minitab v10). Prior to multivariate analysis, to allow for an overall effect of size, all the morphometric measurements listed above, with the exception of the two indices of snout curvature, were standardised for fish size using the equation of Senar *et al.* (1994):

$$Y'_i = \log_{10} Y_i - b(\log_{10} L_i - \log_{10} X)$$

where:

L_i = fork length for fish i (mm)

X = mean forklength (mm)

Y'_i = size-corrected morphometric variable value for fish i (mm)

Y_i = the uncorrected variable value for fish i (mm)

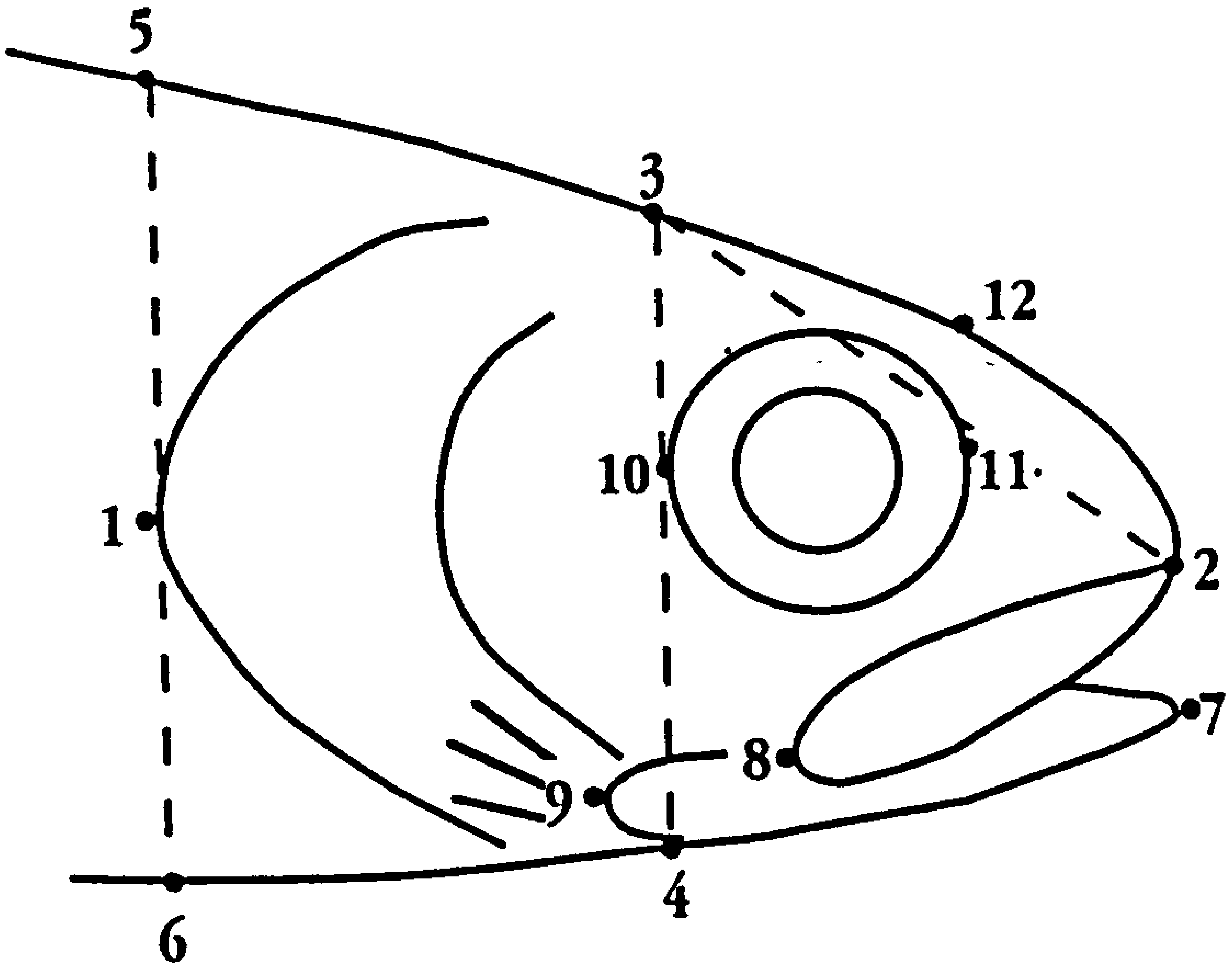

Figure 2.3 Morphometric measurements used: 1-2 = Head length, 3-4 = Head depth at eye, 5-6 = Head depth at operculum, 7-9 = Lower jaw length, 2-8 = Maxillary bone length, 10-11 = eye diameter. Indices of snout curvature, the distance from 2-3 via 12 by 2-3 and snout bluntness, the greatest tangential distance between lines 2-3 and 2-3 via 12 were also derived. Jaw width at point 4 and pectoral fin length were also measured.

b = the pooled regression coefficient of $\log_{10} Y$ on $\log_{10} L$ (for all fish combined)

As snout curvature was not dependent on fish length this variable was not corrected for length.

The effectiveness of standardisation was checked by ensuring that the size corrected variables were not themselves correlated with fork length. The standardised scores were then used, firstly, in a multivariate discriminant analysis (in SPSS) to determine if the three a priori groupings could be distinguished on the basis of the multivariate morphometric data and secondly, to derive a discriminant function for the two cryptically coloured groups.

Dietary analysis

Fish were collected during October and November 1994 and 1995 using multi-mesh survey gill nets set at a variety of depths set at the mouth of the River Gaur and in the general area of Dall Bay. All charr caught were retained and frozen within 6 hrs of capture. On thawing, stomach contents were removed and stored individually in 70% ethanol whereafter each was examined under a binocular dissecting microscope. Each prey item was recorded on a presence / absence basis and expressed as % occurrence of all fish examined. The stomachs from 71 brightly coloured charr, 40 cryptically-coloured Gaur spawning fish and 35 cryptically coloured Dall spawning fish were examined in this way.

Length at age

In order to compare growth patterns, the size and age of charr caught using multi-paneled gill nets in October and November was determined. Overall, 196 brightly-coloured fish, 140 cryptically-coloured Gaur spawning charr and 120 cryptically-coloured Dall spawning charr were examined. Otoliths were removed for age determination and stored in individually labelled envelopes. The external faces of otoliths were ground using fine (1000 grit) aluminium grinding powder to increase the clarity of annuli. Annuli were counted by viewing the external face of the otoliths laterally, immersed in glycerol, illuminated from below under a compound microscope at 400x magnification. Verification of the results obtained by this ageing technique was made by comparison of the results obtained by a second person experienced in the reading of charr otoliths (Janice Fletcher, Institute of Freshwater Ecology, Windermere). Both sets of results agreed closely. Fork lengths of each fish were recorded to the nearest mm.

2.3 Results

Morphological characterisation of head structure

Multivariate discriminant analysis of standardised scores of 10 measured characters confirmed the distinctness of the three *a priori* groupings based on colour and site of capture. The analysis showed significant discrimination between the three *a priori* groups ($F_{20,168}=14.96$; $p<0.0001$) and between each pair of groups (Table 2.1). To test the robustness of predictive discriminate function, jack-knife analysis was performed on this data set (Table 2.2). The greatest number of mis-assignments arose from assigning brightly-coloured fish to one or other of the cryptically coloured groups (10.5% mis-assignments). All other mis-assignements (13.6% in all) involved cryptically-coloured fish being classified with the brightly coloured category, there being no mis-assignments between the two cryptically coloured groups.

As the brightly coloured morph is in practice easily distinguished from the cryptic types on the base of colour alone, in order to derive a reliable discriminating function to distinguish between the two cryptically-coloured forms (where colour is not a discriminator), a step-wise discriminant analysis was performed using data for the two cryptically-coloured morphs alone. Neither pectoral fin length nor the index of snout bluntness is a statistically significant distinguishing variable (Table 2.3). Maxillary bone length (corrected for size) was the most significant discriminating variable and the inclusion of 4 variables gave a significant and realistic canonical discriminant function (D):

$$D = 14.3\,O - 19.9\,E + 10.1Y + 27.1\,M - 40.4$$

Where:

O = depth at the operculum

E = depth at the eye

Y = eye diameter

M = maxillary bone length

Table 2.1 Between morph separation (squared mahalanobis distribution) using 10 head size variables. Overall separation $F_{20,168}=14.96$; $p<0.0001$. All individual p values<0.0001.

	Cryptic colouration Gaur spawning group	Cryptic colouration Dall spawning group	Coloured fish group
Cryptic colouration Gaur spawning group		11.08	13.66
Cryptic colouration Dall spawning group	13.99		8.54
Coloured fish group	19.27	8.54	

Table 2.2 Classification of Arctic charr morphs from L. Rannoch by "jack knife" discriminant analysis of 10 head morphometric variables.

	criptic forms		coloured form
	River Gaur	Dall bay	Dall bay
cryptic Gaur spawners	27	0	0
cryptic Dall spawners	0	27	4
coloured form	1	3	34
N	28	30	38
% correctly assigned	96.4	90	89.5

Table 2.3 The first step in a stepwise discriminant function showing the significance of each size corrected variable in distinguishing between the two benthic morphs. MAX = maxillary bone length, BJ = bottom jaw length, HDO = head depth at operculum, HDE = head depth at the eye, EYE = eye diameter, SC = snout curvature, JW = bottom jaw width, HL = head length, FIN = pectoral fin length, SB = Snout bluntness.

	$F_{1,56}$	p<
MAX	106.1	0.001
BJ	62	0.001
HDO	36.7	0.001
HDE	33.9	0.001
EYE	18.4	0.001
SC	11.5	0.001
JW	8.6	0.01
HL	7.8	0.01
FIN	1.8	N.S.
SB	0.7	N.S.

Using this discriminant function, 92.9% of cryptically-coloured fish captured at the River Gaur and 90.0% of those captured in Dall Bay were correctly assigned to their *a priori* groupings on the basis of morphometric traits alone. Fig. 2.4 shows the relationship between the discriminant score and the probability of membership of one of the cryptically coloured groupings.

One way analysis of variance of snout bluntness (y/x) showed no significant difference between the two cryptic coloured forms ($F_{1,56}$ = 0.65, p=0.423, mean ± S. E. 0.188± 0.02 Gaur spawning cryptic charr and 0.138 ± 0.021 Dall spawning charr). However, the index of snout curvature did differ between cryptic forms ($F_{1,56}$ = 11.67, p,0.001; 1.08± Gaur spawning cryptic form and 1.10 ± 0.030 for the Dall bay spawning cryptic form). Pectoral fin length did not differ significantly between groups in either gradient or elevation of regression (Table 2.4). Of the other variables, only head depth at the operculum showed a significant difference in regression gradient, with the less robust cryptic form having a smaller gradient but a higher intercept than the more robust cryptic form. All of the other variables had non-significant differences in regression gradients, but highly significant differences in regression elevation, the head measurements of the cryptically coloured form collected from Dall Bay being consistently larger for a given fork length than the smaller headed River Gaur morph.

Table 2.4 Covariance analysis of morphometric variables (prior to size correction) of cryptic colouration charr spawning at the River Gaur and Dall bay, α= intercept of regression line, β= gradient of regression line. Abbreviations as per Table 2.3.

Variable	Gradient		Elevation		Gaur spawners		Dall spawners	
	$F_{1,54}$	P	$F_{1,55}$	P	α	β	α	β
HL	0.55	0.46	14.8	<0.001	1.11	0.216	-0.75	0.248
HDE	1.68	0.20	36.0	<0.001	-1.84	0.137	-3.74	0.163
HDO	19.1	<0.001	16.4	<0.001	8.60	0.136	-9.67	0.248
EYE	0.55	0.46	106.8	<0.001	3.24	0.351	5.14	0.030
MAX	3.46	0.07	58.9	<0.001	-3.86	0.108	-5.48	0.144
BJ	0.98	0.33	12.5	<0.001	-3.98	0.144	-3.60	0.169
JW	3.00	0.09	3.51	0.07	-2.37	0.094	-6.41	0.121
FIN	0.88	0.23	58.9	<0.001				

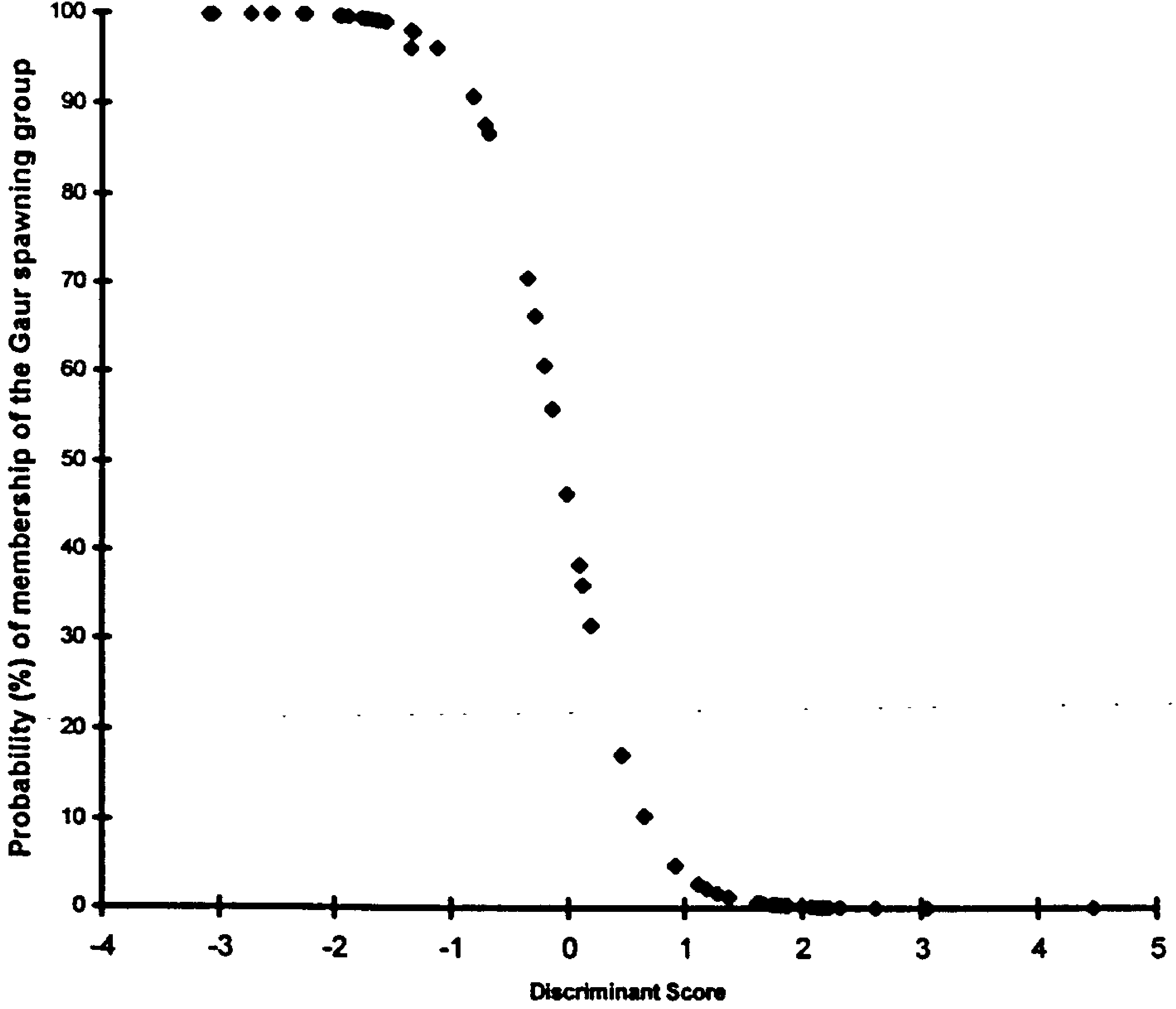

Figure 2.4 Discriminant function score (derived from equation 2) plotted against probability of membership of the Gaur spawning, cryptic coloured charr grouping.

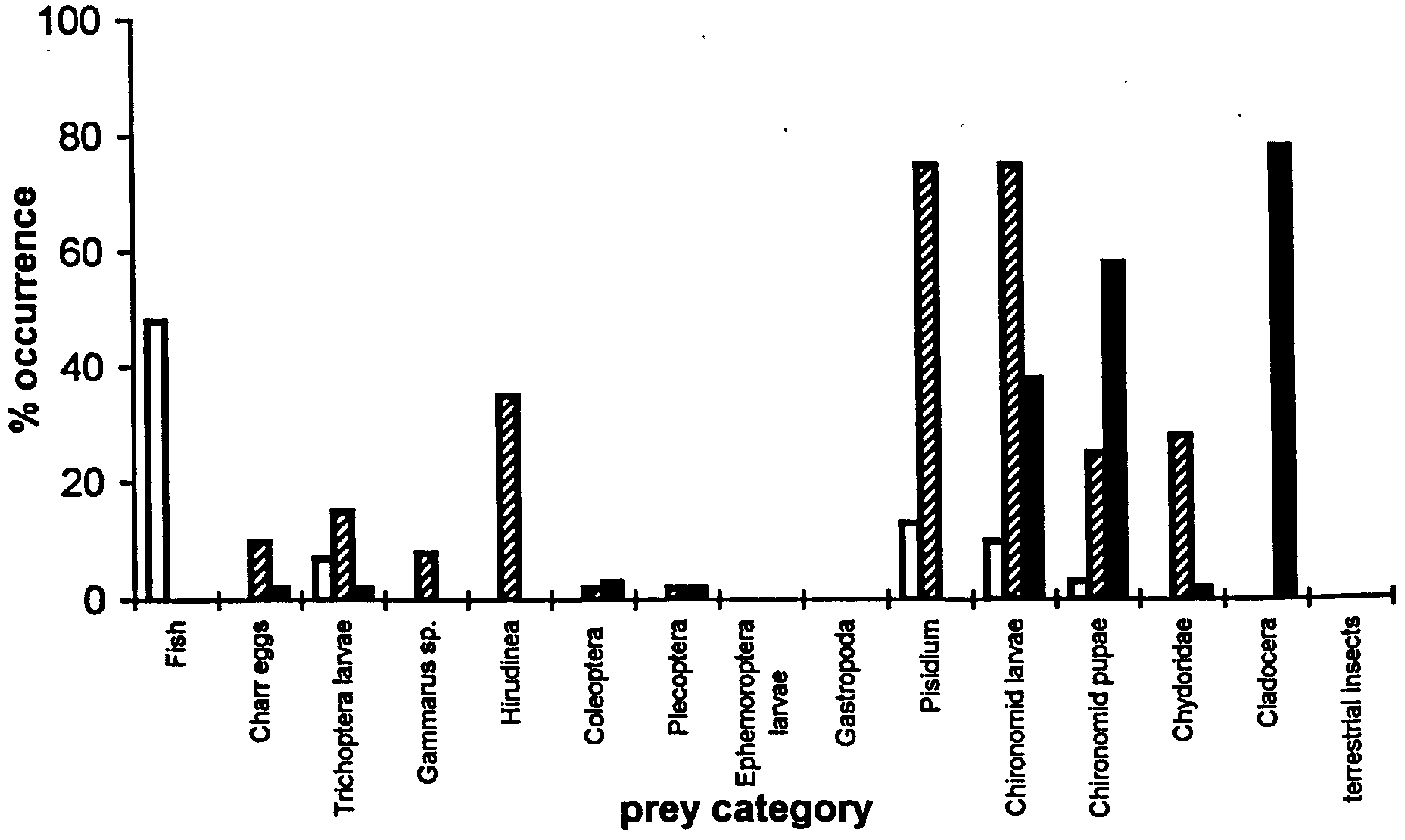

Figure 2.5 Percentage occurrence of prey items identified in charr from L. Rannoch during summer and autumn. coloured charr = ■, cryptically coloured Dall spawning charr = □, cryptically coloured Gaur spawning charr charr = stippled bars.

Diet

Clear dietary differences were apparent amongst the three morphs (Fig. 2.5). Only the highly coloured fish contained non- benthic cladocerans (*Bosmina* and *Daphnia* sp.) which were the predominant prey items (present in 78% of fish) together with chironomid larvae and pupae. Cryptically coloured Gaur spawners also consumed mostly chironomid larvae and the bivalve *Pisidium* sp., these prey types being present, usually in large numbers, in 75% of all individuals examined. Benthic cladocera (*Chydoridae* sp.) and *Hirudinea* were found in 28 and 35% of this form of charr respectively. Cryptically coloured, Dall-spawning fish were the only morph that had consumed other fish, this being their predominant prey. There was a clear dietary shift with size, fish below 16cm consuming benthic invertebrates similar to those present in the cryptically coloured Gaur spawning fish and fish of a greater size being entirely piscivorous (chapter 6).

Length at age

The brightly coloured form and the cryptically coloured Gaur spawning form show similar patterns of mean length with age (Fig. 2.6), with rapid growth in early years, particularly in the latter group, which grows little after age 3+. The brightly coloured form showed slight increases in length in successive years after rapid growth as a juvenile, but never attained the length of the cryptically coloured Gaur spawners. The cryptically coloured Dall spawners were much smaller than the other two forms in their early years, but they lived longer and attained significantly larger sizes at ages not seen in the other two morphs.

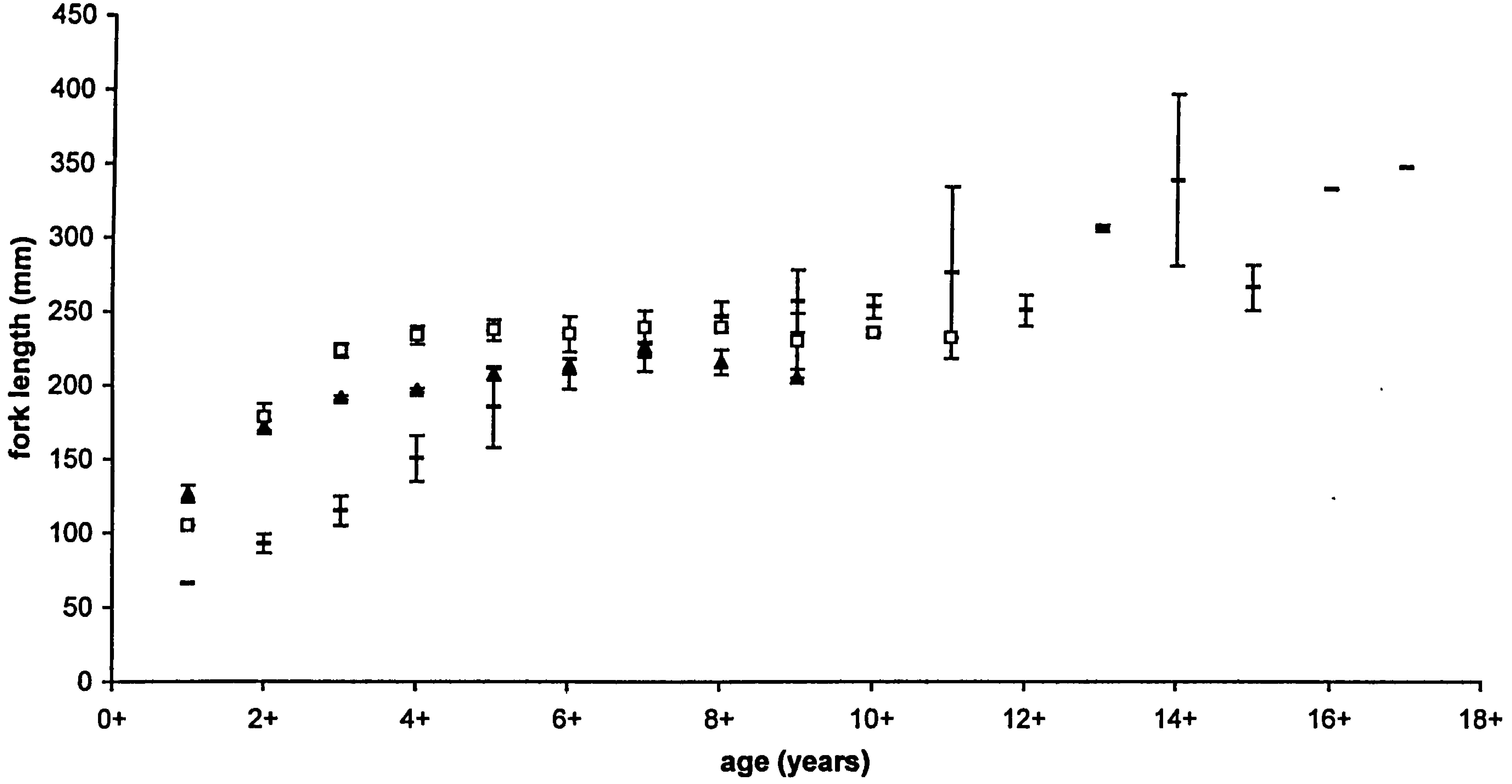

Figure 2.6 Length at age (mean ± s.e.) of each L. Rannoch charr population. (coloured = ▲, cryptically coloured Dall spawners = –, cryptically coloured Gaur spawners = □).

2.4 Discussion

The data presented here suggest that there are at least three discrete morphs of Arctic charr living in sympatry in Loch Rannoch, rather than just the two described by Walker *et al.* (1988). At least over the size ranges used in these analyses, these three morphs can be defined and distinguished on the basis of head morphometric variables alone. The pelagic form of Walker *et al.* (1988) can be distinguished from the other two by its colouration and general body shape. The other two morphs are similar in coloration, both being cryptic, but differ with respect to several head measurements that are independent of overall size. Thus, head length, head depth at two points, eye diameter, jaw length and width and snout curvature all differ significantly between cryptically coloured charr from the two collection sites, with the form from Dall Bay having a longer, deeper head, wider longer jaw and larger eyes. The effectiveness of the canonical discriminant function derived from size-corrected head measurements suggests strongly that these are two discrete morphological groups rather than two ends of a continuum.

In addition to these differences in head morphology, the three categories of charr identified on the basis of colour and site of capture also differed in trophic ecology and growth characteristics. As documented by Walker *et al.* (1988), the brightly-coloured form fed entirely on zooplankton and thus can be termed the planktivorous morph. The cryptically-coloured form that spawns in the Dall Bay area and also throughout the east basin of the loch (Fig. 2.1) has a very robust jaw and head structure. Since this study has shown that a significant proportion of its diet as an adult includes other fish, in addition to some of the larger benthic macro-invertebrate species, it is termed the piscivorous morph. The cryptic colouration form that spawns in the River Gaur is intermediate in relative head and jaw structure size and robustness with the other two forms described here. It feeds upon benthic macro-invertebrates: thus I will refer to this form as the benthivorous morph. On the basis of diet, this form is comparable to the benthic morph described by Walker *et al.* (1988) and Gardiner *et al.* (1988).

Further confirmation of the existence of three distinct morphs is given by the clear differences in length at age amongst them. Interestingly, the greatest difference in patterns of growth was found between the two cryptic coloured forms with the piscivorous fish growing much more slowly, but over a longer period and so to a potentially larger mean size.

Morphologically distinct sub-groups living in sympatry have been described for a number of fish species, most notably in the threespined stickleback *Gasterosteus aculeatus* L. (Lavin and McPhail, 1985) (but see Smith and Skulason, 1996 for others). Amongst Arctic charr, very distinct bimodal size frequency distributions amongst non-anadromous, sexually mature fish have commonly been reported (see Savvaitova, 1969; Nyman *et al.*, 1981; Nordeng, 1983; Klemetsen *et al.*, 1985; Riget *et al.*, 1986; Parker and Johnson, 1991). The lower modal group is formed by smaller, sexually mature charr often described as the dwarf form. These charr typically reach sexual maturity at a small size, retain parr marks to sexual maturity and most frequently are found to feed upon benthos. The so-called normal form constitutes the upper mode of the size frequency distribution of such bimodal size frequency distributions. Such fish are distinguished by reaching sexual maturity at a larger size, the loss of parr marks at maturity and frequently by diet differences. In some systems, anadromous charr constitute a third distinct size frequency modal grouping of larger size than the "normal" resident group and usually also differ in colour (Nordeng, 1983). For at least two systems where these size forms occur in sympatry, rearing and transplantation studies have shown that each of the three forms produce offspring which ultimately segregate into all three forms (Nordeng, 1983; Hindar and Johnson, 1993). Further, Nordeng's experiments demonstrated transformation of some individuals from small resident to both large resident and anadromous and from large resident to anadromous form (Nordeng, 1983). Thus this commonly reported polymorphism represents the phenotypic outcome of a series of developmental pathways and developmental speed options expressed by individuals from a common gene pool (see also Hindar and Jonsson, 1993 and Thorpe, 1994 a and b) which is not fixed and could change with time. Because of this we would argue that apparently differing forms can not be regarded as morphs but should be termed ontogenetic forms.

Further, we would argue that the morphs we describe here from L. Rannoch are inherently different in type from these ontogenetic forms for four reasons. Firstly, and unlike ontogenetic forms, the morphs described here do not differ substantially in body size and maturing fish do not form multi-modal size frequency distributions (chapter 5). Thus an obvious developmental transition from one form to another does not exist. Secondly, the head shape characters that clearly discriminate between Rannoch morphs are so extreme in similar sized fish that transition from one head shape form to another during an individuals lifetime is inconceivable. Thirdly, unpublished data from rearing experiments of the benthivorous and planktivorous Rannoch morphs (Adams and Huntingford, unpublished) has shown within morph conservation of head shape differences (Adams and Huntingford, unpublished data). Fourthly there is genetic evidence that the benthivorous and planktivorous morphs are genetically distinct (Hartley *et al.*, 1992). Thus the charr morphs from L. Rannoch described here appear to be more like the true morphs described for Thingvallavatn, Iceland (Snorrason *et al.*, 1989) where between morph morphometric character differences are fixed and inherited (Snorrason *et al.*, 1994).

[1]CHAPTER 3 - TROPHIC POLYMORPHISM IN THE ARCTIC CHARR OF LOCH ERICHT.

3.1. Introduction

Trophic polymorphism is the phenomenon whereby a single species exhibits two or more forms each of which possesses a distinct morphology which is an adaptation to utilise a particular trophic resource. Although this phenomenon is recorded in numerous vertebrates in particular amphibians and birds (see review by Smith and Skúlason, 1996) it is most common in freshwater fish. Although several instances of multiple occurring trophic morphs exist e.g. in the *Barbus* sp. of Lake Tana, Ethiopia (Nagelkerke *et al.*, 1994) and the cichlids of the African Great Lakes (Meyer, 1993) more commonly two trophic morphs occur. Typically these are a morph which utilises the pelagic zone and feeds on zooplankton and morph which occupies the epibenthic zone and feeds on zoobenthos. Such morphs have been recorded in the threespined stickleback *Gasterosteus aculeatus*, (Cresko and Baker, 1996; Lavin and McPhail, 1986), Kokanee (freshwater resident) *Oncorhynchus nerka* (Kurenkov, 1977) and the bluegill sunfish *Lepomis macrochirus* (Robinson *et al.*, 1993). In each instance, morphological adaptations appear to be similar with planktivorous morphs usually possessing fusiform bodies with delicate head and jaw features and fine, long gill rakers and benthivorous morphs usually possessing deeper bodies with robust heads and jaws and fewer, shorter gill rakers.

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[1] This chapter is the basis of a submitted manuscript: Fraser, D., Adams, C. E. and Huntingford, F. A. The ecology of a dimorphic Arctic charr population in Loch Ericht, Scotland.

The salmonid species which is reported most extensively as exhibiting trophic polymorphism is the Arctic charr *Salvelinus alpinus* (L.) (Johnson, 1980). As well as demonstrating variation in trophic morphology, charr exhibit great variation in life history characteristics such as age and length at maturity and frequency of spawning (Johnson, 1980). Several Scandinavian lakes have been demonstrated to contain two forms of charr, a small form (commonly referred to as a "dwarf") typically occupying a benthic habitat and nominally a "normal" form that reaches a larger size, feeding in the pelagic zone (e.g. Hindar and Jonsson, 1982; Klemetsen and Grotnes, 1980). Thingvallavatn, Iceland contains four distinct forms of charr, each with adaptations for life in a specific habitat. The four forms are: a small benthic form, able to utilise the interstitial spaces in the lava substrate of the lake; a large benthic form that feeds on benthic invertebrates; a piscivorous form and a planktivorous form. Each form has a distinctive ecology, morphology and life history strategy (Snorrason *et al.*, 1994).

Only one instance of trophic polymorphism has been documented in Arctic charr in the British Isles. Walker *et al.*, 1988 and Gardner *et al.*, 1988 described the occurrence in Loch Rannoch, Scotland of a planktivorous and a benthivorous morph, each differentiated on the basis of habitat, diet, spawning site and morphology. Hartley *et al.* (1992) demonstrated that these two morphs were also genetically distinct. Further analysis of Loch Rannoch charr has demonstrated the occurrence of a third form, a deep-water living piscivore (chapter 2) that differs from the other two morphs both in feeding ecology and in trophic morphology. Dietary differences amongst these three forms has been further confirmed by significantly different helminth parasite faunas (Dorucu *et al.*, 1995). This work demonstrated that planktivorous charr had higher burdens of *Diphyllobothrium* sp. and *Eubothrium salvelini* both of which are transmitted by ingesting planktonic copepods. Benthivorous fish were however relatively parasite free although they did have higher burdens of *Diplostomum* sp. which are known to be transmitted by gastropods. Piscivorous charr had similar parasites to planktivorous fish although they occurred at lower frequencies in piscivorous individuals.

Loch Ericht is a large lake (18.62 km^2) within the same catchment as Loch Rannoch (Fig 1.3). As with Loch Rannoch, there is considerable heterogeneity in habitat, and low species diversity; lake characteristics which may initiate or support the existence of polymorphism in its Arctic charr population (Sandlund *et al.*, 1992). The aim of the work presented here is to test the hypothesis that as with Loch Rannoch, the biotic and habitat conditions in Loch Ericht are able to support trophic polymorphism in its previously undescribed Arctic charr population.

3.2. Materials and methods

Study site

Loch Ericht (GR 56° 50′N 4° 20′W) is situated in Tayside and Highland regions (Fig. 1.3). It is a deep, oligotrophic fjord-like loch, at 352m altitude. It is 25 km long and has a maximum width of 2 km towards its southern end. Its maximum depth is 156m (Murray and Pullar, 1910) although the water level is subject to fluctuations of several metres due to the loch being utilised for Hydro-electricity generation. As well as charr, the loch contains brown trout, *Salmo trutta* threespine sticklebacks, *Gasterosteus aculeatus*, minnows, *Phoxinus phoxinus* (L.) and eels *Anguilla anguilla* (L.) (Campbell, 1979).

Capture of fish

Fish were collected by multi-panelled, benthic gill nets set at 10-20m, 25-30m and 40-50m depth. A single, 35m long by 1.5m deep, multi-panelled benthic gill net (8 panels, knot to knot mesh sizes ranging from 8-50 mm) was set at each depth and fished for a period of approximately 48h. Fish caught were retained and frozen within 6h of removal from the net. Sampling was conducted once in May, August and September and twice in October 1996.

Sampling revealed what appeared to be two forms of charr (Fig. 3.1), a brightly coloured streamlined form similar in appearance to the planktivorous form of Loch Rannoch (Walker *et al.*, 1988; Gardner *et al.*, 1988) and a pale form similar to the piscivorous form in Loch Rannoch (Adams *et al.*, 1998).

Post-mortem procedure

Fish were removed from the freezer and allowed to thaw overnight. A photograph of the head of each fish was taken from the right side against a 1 cm grid for calibration. Fork length (to the nearest mm) and weight (to the nearest gram) were also recorded.

Fig. 3.1 Arctic charr from L. Ericht. Top two fish = Pale (piscivorous) charr, bottom three fish = coloured (planktivorous) charr.

To enable diet determination, the stomach contents of each fish was removed and individually stored in 70% ethanol, where at a later date they were examined under a binocular dissecting microscope. Diet was expressed as percentage occurrence of each prey item in the stomachs of all fish examined (Hyslop, 1980). Otoliths were removed for age determination and stored in individually labelled envelopes. The external faces of otoliths were ground using fine (1000 grit) aluminium grinding powder to increase the clarity of annuli. Annuli were counted by viewing the external face of the otoliths laterally, immersed in glycerol, illuminated from below under a compound microscope at 400x magnification.

Morphometric analysis

In order to determine quantitatively if variability in morphology amongst the charr examined was non-continuous, several dimensions of head and body size were measured. Measurements (± 0.005 mm), taken from prints from post mortem photographs were made using a computerised digitising pad (Fig. 3.2). Data collected from 35 coloured and 26 pale charr was then subjected to univariate analysis (analysis of covariance) and multivariate analysis (principal component analysis (PCA) and discriminate analysis) using colour as an *a priori* group assignment. Prior to multivariate analysis only, in order to standardise each of the morphometric variables for size, the equation of Sennar *et al.* (1994) was employed:

$$Y'_i = \log_{10} Y_i - b(\log_{10} L_i - \log_{10} X)$$

where:

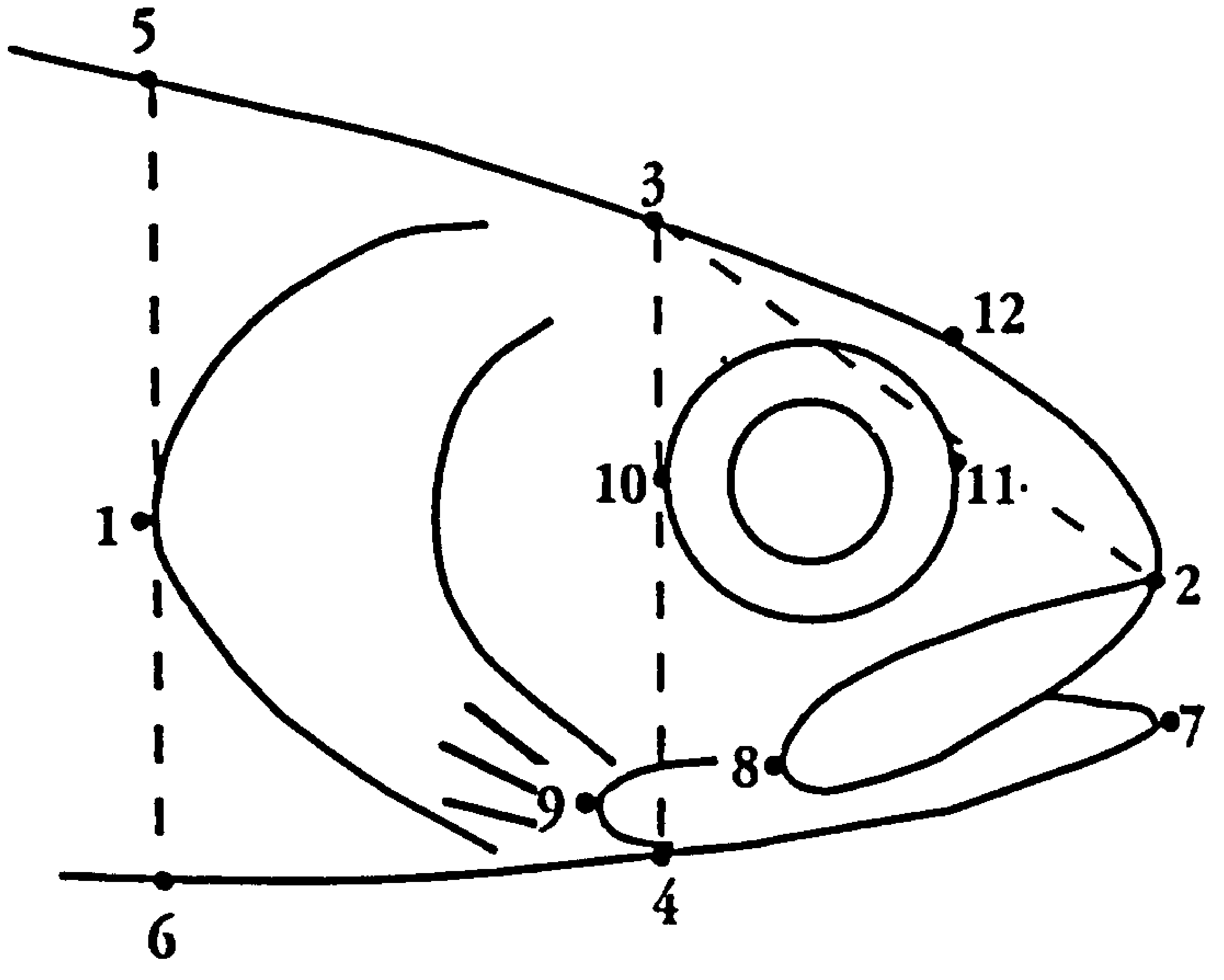

Figure 3.2 Morphometric measurements used: 1-2- Head length, 3-4- Head depth at eye, 5-6- Head depth at operculum, 7-9- Lower jaw length, 2-8- Maxillary bone length, 10-11- eye diameter. An index of snout curvature was also derived by dividing the distance from 2-3 via 12 by 2-3. Jaw width at point 4 was also measured.

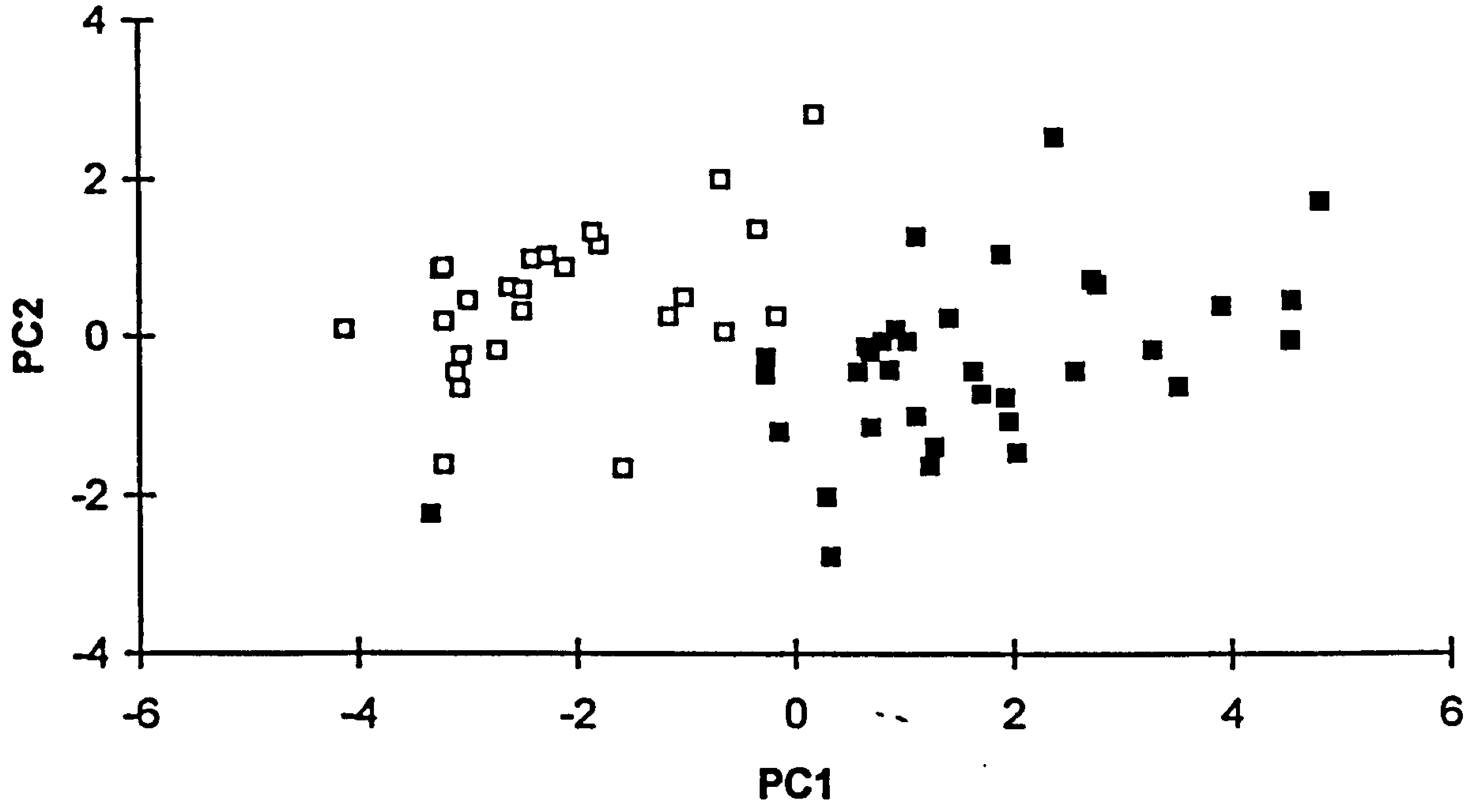

Figure 3.3 Distribution of L. Ericht charr on PC 1 and PC 2 of a principal components analysis using morphometric variables in Fig. 3.2. PC 1 is a size vector with all variables similar in sign and magnitude apart from eye diameter and snout curvature. PC 2 is contributed to mainly by eye diameter and fin length (+) and jaw width and snout curvature (-) (pale charr = □, coloured charr = ■).

L_i = fork length for fish i (mm)

X = mean forklength (mm)

Y'_i = size-corrected morphometric variable value for fish i (mm)

Y_i = the uncorrected variable value for fish i (mm)

b = the pooled regression coefficient of $\log_{10}$ Y on $\log_{10}$ L (for all fish combined)

As snout curvature was not dependent on fish length, this variable was not corrected for length.

3.3 Results

Morphometric analysis

Covariance analysis of uncorrected character length on fork length for both charr groups (Table 3.1) indicated significant differences (Tukey HSD test, $P<0.05$) in slope of regression lines for all characters except head depth at the operculum and pectoral fin length. Head depth at the operculum (HDO) does however differ significantly in elevation of regression line ($P<0.05$). No significant difference was found in elevation of pectoral fin length (FIN) on fork length regressions for the two groups. Eye diameter was the only character that was significantly smaller for a given length in pale than coloured fish.

Principal component analysis on size corrected morphometric variables (Table 3.2) revealed that PC 1 accounted for 56.3% of the total variance and is a size vector with the signs (negative) and magnitudes of all its coefficients very similar with the exception of eye diameter and snout curvature which had a positive value. PC 2 contributed to 17.2% of the total variance (73.5% of the remaining variance). Eye diameter and fin length contributed strongly to this component and are contrasted most strongly with jaw width, snout curvature and head length the remaining scores contributed little to this component. Component scores were calculated for each individual fish on PC 1-4. The distributions of pale and coloured fish on both PC 1 and PC 2 were significantly different (Mann-Whitney-U test, $U_{1,59} = 24$, $P < 0.0001$; $U_{1,59} = 241$, $P < 0.005$ respectively; Fig. 3.3) but did not differ on PC 3 and 4.

Discriminant analysis of pale and coloured charr indicated that the two groups of charr could be successfully discriminated from each other on the basis of the nine morphometric variables recorded. 98% of fish were assigned to the correct *a priori* assignment group with only one coloured fish misclassified. The most discriminating variables at step one of the stepwise discriminant function (Table 3.2) were head length, maxillary bone length and jaw width. Jaw width as a discriminator on its own gave correct assignment of 98% of fish to their *a priori* groups. Neither pectoral fin length or index of snout curvature were significant discriminating variables. Inclusion of all nine variables did not increase the proportion of correctly assigned fish with one coloured fish misclassified as a pale fish.

Table 3.1 Covariance analysis of head character dimensions (prior to size correction) on fork length for pale and coloured Arctic charr from L. Ericht. α= intercept of regression line, β= gradient of regression line. Abbreviations as in Table 2.3.

Variable	GRADIENT		ELEVATION		Coloured		Pale	
	$F_{1,57}$	P	$F_{1,58}$	P	α	β	α	β
HDO	2.880	=0.095	5.2	<0.05	-2.16	0.193	-5.90	0.224
HDE	7.680	<0.01			0.73	0.126	-1.38	- 0.153
HL	36.35	<0.001			3.87	0.193	-1.43	0.265
MAX	9.150	<0.005			-0.74	0.101	-2.86	0.138
BJ	6.460	<0.05			-2.53	0.135	-4.24	0.167
EYE	10.66	<0.005			1.75	0.043	3.59	0.027
FIN	0.130	=0.716	1.18	=0.282	-6.87	0.218	-7.16	0.224
JW	62.28	<0.001			0.21	0.043	-3.35	0.084

Table 3.2 Eigenvector coefficients for the nine size corrected head character dimensions analysed and the relative significance of the inclusion of each size corrected dimension at step one of the stepwise discriminant analysis.

Variable	PC1	PC2	PC3	PC4	$F_{1,59}$	P value
HDO	-0.261	0.270	-0.851	0.162	3.0	0.0890
HDE	-0.406	0.047	-0.047	0.220	45.5	0.0001
HL	-0.412	-0.170	0.153	0.055	189.3	0.0001
SNOUT	0.242	-0.432	-0.142	0.757	6.80	0.0117
MAX	-0.425	-0.052	0.155	0.114	104.4	0.0001
BJ	-0.411	0.019	0.251	0.040	69.5	0.0001
EYE	0.163	0.569	0.369	0.560	22.2	0.0001
FIN	-0.273	0.431	0.051	0.061	2.9	0.0928
JW	-0.304	-0.443	0.071	0.129	103.5	0.0001
% variance	56.3	17.20	7.600	6.300		

Dietary analysis

Clear differences were apparent in the diets of the two groups (Fig. 3.4) with 40% of stomachs of the pale group containing other fish as opposed to only one of the coloured charr stomachs. Coloured charr predominantly consumed zooplankton (mainly cladocera) which was present in 48% of individuals. Zooplankton was not present in the diet of the pale group. Benthic invertebrates were more prevalent in stomachs of pale than coloured charr with Trichoptera larvae and Hirudinea occurring only in pale charr (25% and 8% of individuals respectively). The amphipod *Gammarus* sp. and the bivalve *Pisidium* sp although also occurring in coloured individuals, occured at twice this frequency in pale charr. Piscivory was only noted in pale charr of fork length 16 cm or more with all fish found in pale charr being other charr, several of which could be identified as pale charr.

Growth patterns

Comparison of length at age between the two forms (Fig. 3.5) indicated that pale charr were smaller than coloured charr below age 8+, whereafter pale fish attained sizes in excess of those attained by coloured fish in which growth levels off at age 5+ corresponding to an asymptotic length, L_α of 210mm, as given by the von Bertalanffy growth equation. Comparisons of growth parameters between the two groups as determined by the von-Bertalanffy equation was not possible as pale fish showed a poor fit to this model.

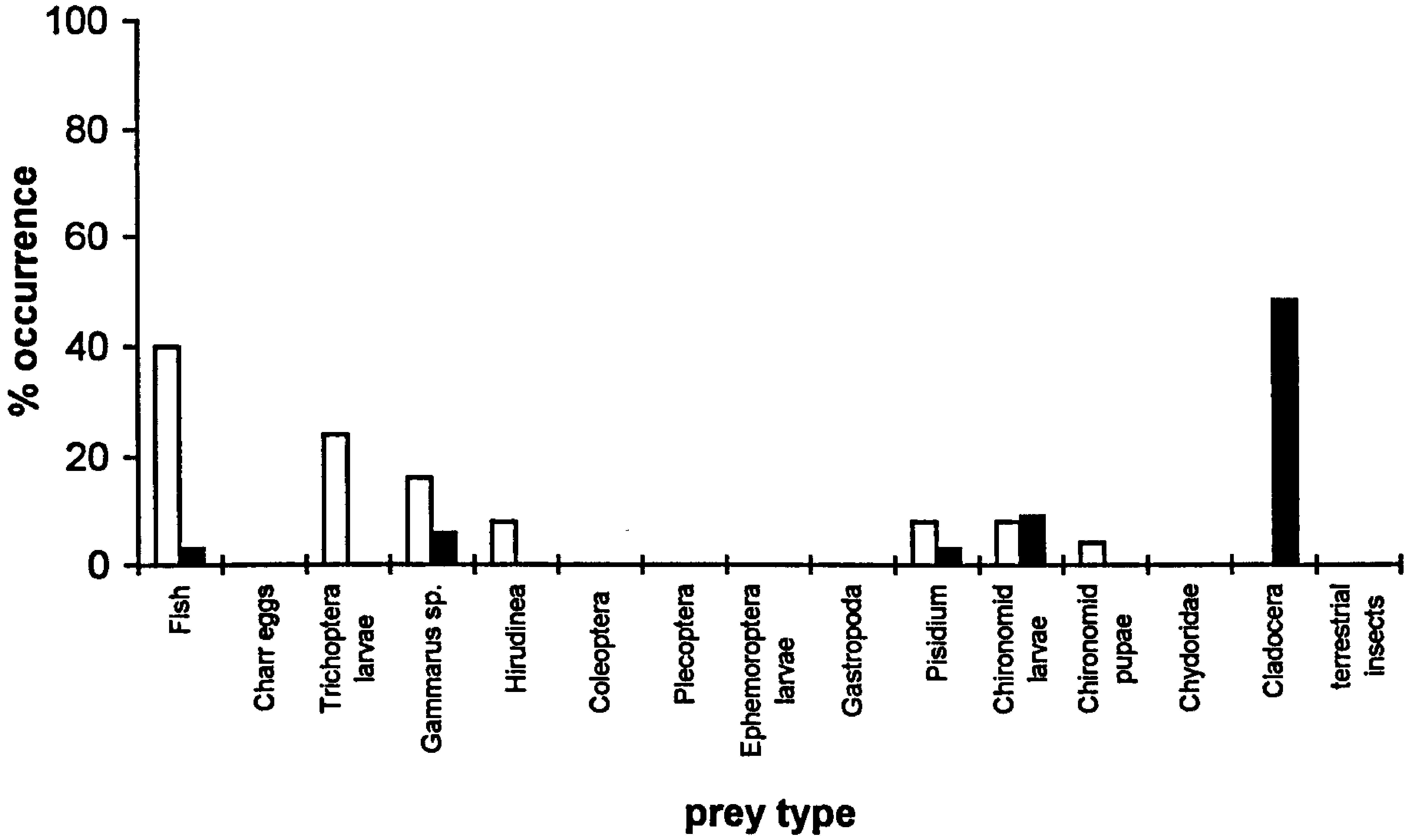

Figure 3.4 Percentage occurrence of prey items identified in L. Ericht coloured charr (■) and pale charr (□).

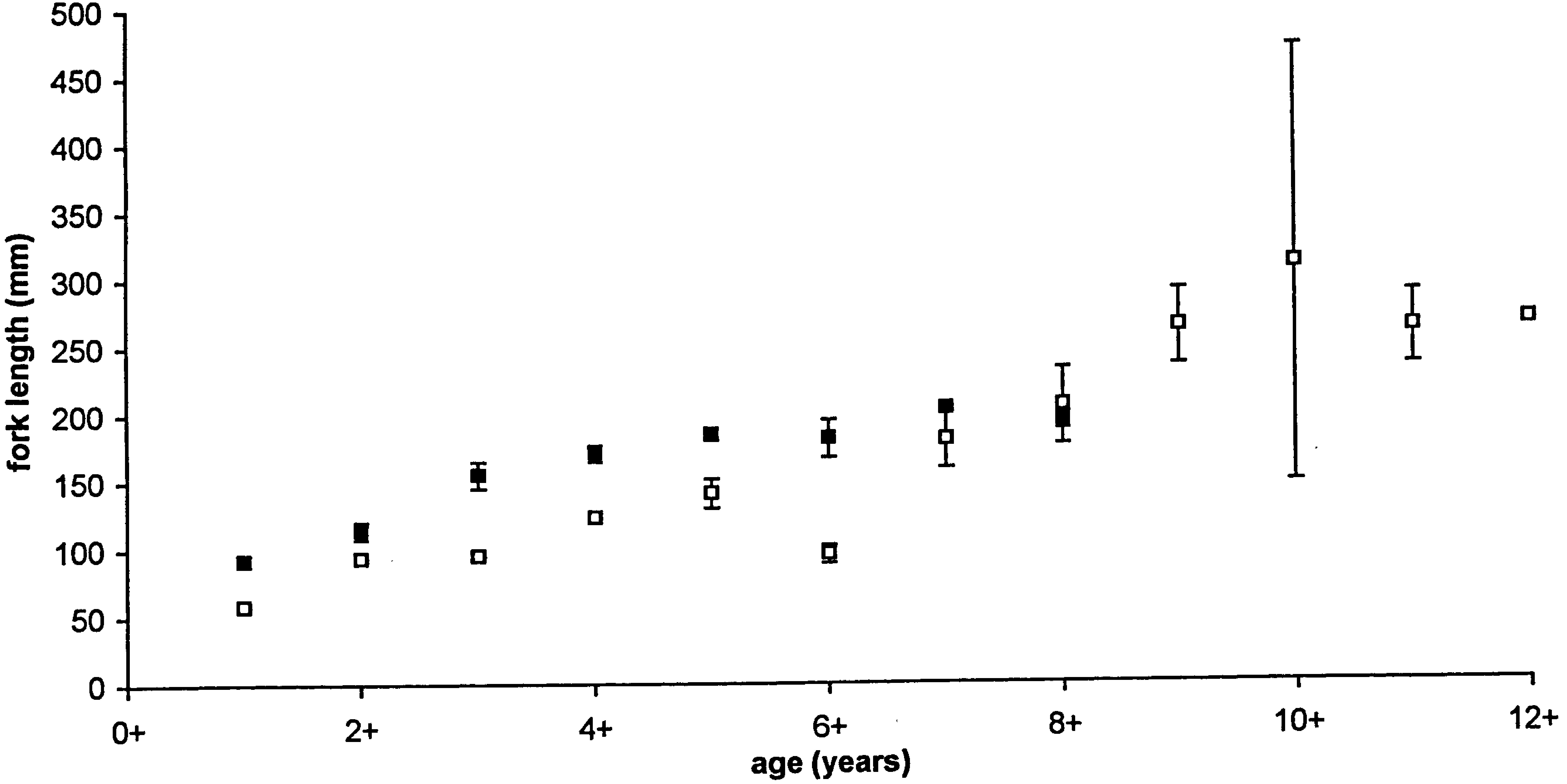

Figure 3.5 Length at age (mean ± s.e.) of charr from L. Ericht (pale charr = □, coloured charr = ■).

3.4 Discussion

The morphometric analysis clearly demonstrates that two discrete morphological groups of charr exist in Loch Ericht, these differences occurring independently of fish size. In addition to the differences in colouration and relative head size and shape between pale and coloured charr, differences in diet demonstrate that this dimorphism has a trophic basis. Thus, the pale form at sizes possibly greater than 16 cm consume mainly fish (including other charr) and possess large robust head features, whereas the coloured form, which consumes zooplankton, has a more streamlined body and head and finer jaw features.

As well as feeding on pelagic organisms, the absence of coloured charr in benthic gill net catches in May, August and September suggests that these fish almost entirely occupy the pelagic zone during this period. Increased catches of gravid and running-ripe coloured charr during October suggest that this form was migrating into the littoral zone to spawn. Similar seasonal catch vulnerabilities of pelagically feeding charr have been reported by Parker and Johnson (1991) and Sparholt (1985). Although it is difficult to draw any conclusions about habitat preferences of the pale charr due to the extreme scarcity of these fish in catches, there was a tendency for pale charr to be caught at greater depth than coloured charr (chapter 6). That the pale charr are better adapted and prefer deeper water is supported by the observation that when raised in gill nets from depth, piscivorous charr invariably had hugely distended swim bladders as a result of being unable to equilibrate the volume of air in their swim bladders to the lowered water pressure and when released, floated upside down at the surface despite attempting to right themselves. This was not observed in the coloured charr raised from the same depth. Similarly, Ihssen and Tait (1974) demonstrated experimentally that offspring of two allopatric populations of Lake trout *Salvelinus namaycush* each of which inhabited a different depth in their respective lake, when reared under identical conditions, showed significant differences in their ability to retain swim bladder gas. Thus, the population which occurred at greater depth was able to retain swim bladder gas more efficiently.

If we compare the two forms of charr in Loch Ericht with the three forms in adjacent Loch Rannoch, there are close ecological parallels between the L. Ericht coloured form and the L. Rannoch planktivorous form and between the L. Ericht pale form and the L. Rannoch piscivorous form in terms of diet, habitat, colouration, morphology and growth patterns. It therefore seems reasonable to adopt the nomenclature of chapter 2 and Adams *et al.* (1998) and refer to the Ericht coloured and pale forms as the Ericht planktivorous form and piscivorous forms respectively.

A number of reports of dimorphic or polymorphic charr populations demonstrate the existence of a small benthic form (e.g. Hindar and Jonsson, 1982; Jonsson *et al.*, 1988). Such a morph has not been found to exist in lochs Ericht or Rannoch where the non-pelagic forms, while displaying parr marks when mature and showing relatively slow growth in early years as with individuals from small benthic populations (e.g. Sandlund *et al.*, 1992; Kristoffersen and Klemetsen, 1991), attain sizes much greater than those of the planktivorous form. The reason for the planktivorous form showing decreased growth in older age groups and inferior longevity may be a consequence of individuals being unable to forage profitably on zooplankton as they increase their size (Snorrason *et al.*, 1996).

It is interesting to note that it is the deeper water, bottom feeding charr form with the more robust trophic morphology that becomes piscivorous in Loch Ericht. This is in contrast to the piscivorous form of Thingvallavatn which has a similar delicate head structure to the Thingvallavatn planktivorous form and indeed these two forms are thought to arise from alternative ontogenetic routes of a single morphotype (Sandlund *et al.*, 1992). Thus it appears that there is more than one ontogenetic route to piscivory. These differences may be due to the different adaptations required to feed on threespined sticklebacks which are abundant in Thingvallavatn and are the main prey item of the piscivorous form. Threespined sticklebacks are not abundant in Loch Ericht (unpublished data, this study) and piscivorous charr therefore feed mainly on other charr. In this study, sticklebacks were only found in the diet of one fish, a planktivorous individual.

As yet, the degree to which the two forms of Arctic charr discussed here are reproductively and genetically isolated has not been determined. When offspring of two of the three Loch Rannoch morphs (Adams and Huntingford, unpublished data) and the four Thingvallavatn morphs (Skulason *et al.*, 1989) were reared under identical rearing conditions, parental morphologies were inherited, indicating that these polymorphisms have a genetic basis. Such a study of the Loch Ericht morphs would provide strong evidence as to the contribution of environmental and genetic effects. However, the large morphological differences, which are apparent even in the smallest individuals in this study would make it inconceivable that these differences are entirely due to environmental factors. We therefore propose that as with L. Rannoch charr, L. Ericht charr morphs are likely to represent true isolated spawning populations of differing trophic morphology as opposed to charr morphs described in other studies (e.g. Nordeng, 1983; Hindar and Jonsson, 1993) which appear to be consequences of different developmental routes and should therefore be termed ontogenetic morphs (chapter 2; Adams *et al.*, 1998).

CHAPTER 4 - RELATIONSHIP BETWEEN MORPHOLOGY AND FEEDING SPECIALISATION: A COMPARISON OF ARCTIC CHARR FROM LOCHS RANNOCH, ERICHT AND TAY

4.1 Introduction

Several fish species are known to exhibit two or more forms within a single water body. Amongst the most notable examples of this are in whitefish (*Coregonidae*) (Lindsey, 1981; Amundsen, 1988), bluegill and pumpkinseed sunfish *Lepomis macrochiru* and *Lepomis gibbosus* (Ehlinger, 1990; Robinson *et al.*, 1993) and the threespined stickleback *Gasterosteus aculeatus* (McPhail, 1984; Lavin and McPhail, 1986), (see review by Smith and Skúlason, 1996). Typically populations exhibit a benthivorous and a planktivorous form which differ correspondingly in trophic structures such as jaw and gill raker morphology. While some of these polymorphisms appear to be the result of different life history strategies, developmental routes, feeding opportunities or ontogenetic shifts within a single population (eg. Nordeng, 1983; Hindar and Jonsson, 1993) others appear to represent reproductively isolated spawning populations (e.g. Ferguson and Mason, 1981; Snorrason *et al.*, 1994).

Arctic charr is one species which frequently shows within lake variation, the most notable example being the four morphs in Thingvallavatn in Iceland (Sandlund *et al.*, 1992) each of which utilises a specific ecological niche and has corresponding morphological adaptations. The existence of morphs within a single water body give rise to the question as to whether the morphs evolved in separate localities but subsequently invaded a common habitat (allopatric evolution), or, whether they have evolved into the two forms in the lake that they currently inhabit (sympatric evolution). These situations are of particular interest given that many dimorphic or polymorphic populations occur in lakes whose ages are young, having only come into existence after deglaciation, some 10 000 years ago. Examination of these sites is likely to provide insights into the processes of speciation. While numerous morphological studies of pairs of morphs within a single lake exist (McPhail, 1984; Gardner *et al.*, 1988; Sandlund *et al.*, 1992) less attention has been paid to parallel, inter lake comparisons of morph pairs.

The existence of two sympatric morphs of charr (a benthivorous and planktivorous morph) in Loch Rannoch, Scotland has been recognised for some time (Walker *et al.*, 1988) and more recently a third (piscivorous) morph has been identified (chapter 2; Adams *et al.*, 1998). Further studies of two adjacent (Fig. 1.3) and ecologically similar lochs (Table 4.1) within the same catchment have shown that these charr populations differ in the degree of polymorphism that they exhibit. Thus, Loch Ericht has been shown to contain two morphs of charr, a piscivorous and a planktivorous form (chapter 3) whereas initial observations of Loch Tay charr suggested that they comprise only a single form (this study). Details of dietary specialisations are given in chapters 2, 3 and 6.

In this study I aim to examine the morphological relationships of charr morphs exploiting similar trophic niches in different lakes and to explain why the three lakes in question differ in the number of charr morphs present with a view to understanding the evolutionary relationships among them and the selective processes that might have caused their evolution.

4.2 Materials and methods

Capture of fish

Sampling was carried out during 1994-1996 from October 15th to 8th November, the period during which all populations spawn. Charr were also sampled during the summer in L. Tay. Multi-panelled gill nets (8 panels, knot to knot mesh size ranging from 8-50mm) were set at a range of depths for periods of approximately 24h. All charr captured were removed from nets and were frozen within 6 h.

Morphometrics

The procedure for obtaining morphometric data was the same as in chapters 2 and 3 and the morphometric measurements were the same as those used in chapter 3.

Size correction

Prior to multivariate analysis (principal components analysis (PCA) and discriminant analysis), to allow for an overall effect of size, all the morphometric measurements listed above, were standardised for fish size using the equation of Ihssen *et al.* (1981):

$$M_t = M_o (L_m/L_o)^b$$

where

L_o = fork length for individual fish

Table 4.1. Area, mean depth, altitude and alkalinity of the study Lakes (Data from Campbell, 1979).

Loch	Area (ha)	Mean depth (m)	Altitude (m)	Alkalinity (mg $CaCO_3\,l^{-1}$)
Tay	2644	60	106	8.4
Rannoch	1908	51	203	5.4
Ericht	1868	57	351	4.3

L_m = mean fork length for all fish

M_t = size corrected morphometric variable

M_0 = the uncorrected variable

b = the pooled regression coefficient of $\log_e M_0$ on $\log_e L_0$

Gill raker counts

Gill raker dimensions were examined under a dissecting microscope fitted with an eyepiece graticule. The length of the longest gill raker was measured, as was the distance between the longest gill raker and the 8th gill raker along the bottom arch from this. The mean inter raker separation was calculated from this measurement. In addition to these two measurements, the total number of gill rakers was also counted. Both length and separation of gill rakers increased linearly with fork length in all fish groups ($F_{1,103}=33.06$, $p<0.001$; $F_{1,105}=373.74$, $p<0.001$ respectively). Comparisons were therefore made on size corrected values. No significant relationship was found between number of gill rakers and fork length except in Rannoch piscivores ($F_{1,35} = 5.54$; $p<0.05$) where raker number increased with fork length. Gill raker counts were therefore compared without correction. As gill raker data were obtained from fish which were not subjected to morphometric analysis, these were analysed separately and not included in the multivariate analysies.

4.3 Results

Principal component analysis

Means of each size corrected morphometric variable for each fish group used in the PCA are given in Table 4.2. Results of principal components analysis of all size corrected morphometric variables (Table 4.3) revealed that PC1 was a size component with all variables of a similar magnitude and only one variable (snout curvature) with a positive value. Fish with larger heads thus score more negatively on the PC1 axis (Fig 4.1). This axis discriminates to a large extent between the L. Rannoch and L. Ericht piscivorous morphs which score negatively and are not significantly different from each other (Table 4.4) and all other groups, which score positively are significantly different from both the piscivorous forms ($F_{5,226}$=22.22; $p<0.05$) but not from each other. Snout curvature contributes most significantly to PC2, with this variable having a strongly negative score. The next most significant contributor is jaw width which has a positive score. Fish with highly curved snouts and narrow jaws thus score more negatively on this axis. No significant differences were found amongst both L. Ericht morphs and L. Tay fish which score negatively on this axis although these three groups are significantly different from all L. Rannoch morphs,($F_{5,226}$=31.7; $p<0.05$) which score positively. Amongst the L. Rannoch morphs significant differences in PC2 only existed between planktivorous and benthivorous morphs ($F_{5,226}$=31.7; $p<0.05$) indicating that the benthivorous fish had more curved snouts. The largest degree of variability on PC1 and PC2 was shown by the monomorphic L. Tay charr (Table 4.4). PC3 explains 12.8% of the total variance with jaw width and eye diameter being the largest contributors to this component, both having positive

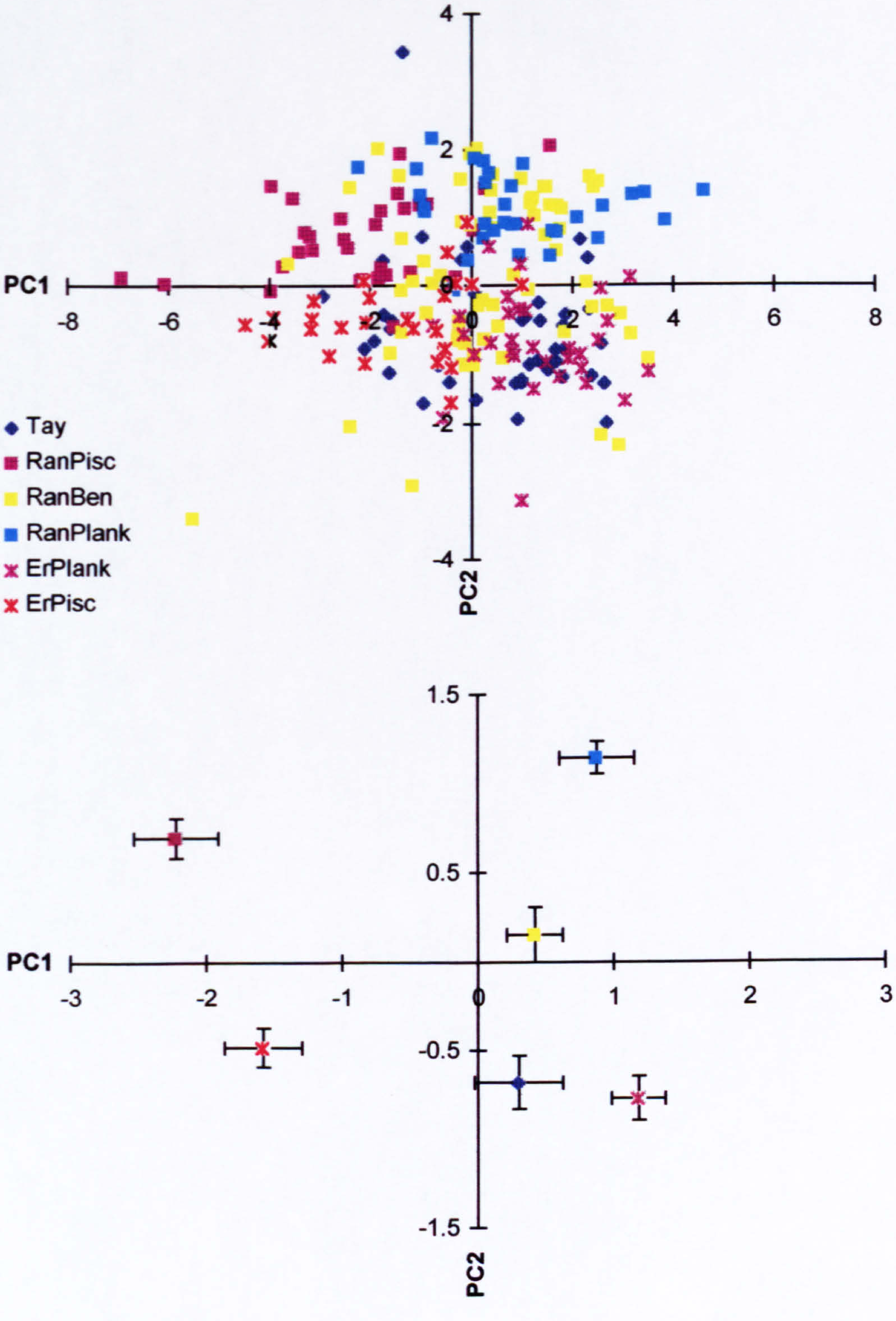

Figure 4.1 Distribution of the six charr populations on PC 1 and PC 2 of a principal components analysis of nine morphometric measurements. Top graph = individual fish; Bottom graph = group means ± s.e.

signs. Pectoral fin length contributes to a similar degree but has a negative sign. Both L. Ericht morphs, the L. Rannoch planktivorous morph and L. Tay fish score negatively on this component and show no significant differences from each other although each is significantly different from the remaining three morphs ($F_{5,226}$=56.55; $p<0.05$), of which L. Tay and L. Rannoch benthivores differ significantly.

Discriminant analysis

Using the 10 morphometric variables as discriminators it was possible to allocate 78.9% of fish to their *a priori* groupings. Loch Tay fish were the most mismatched group (52.4% correctly assigned) followed by L. Rannoch piscivorous and L. Ericht planktivorous (77.3 and 85.7% mismatched respectively; Table 4.5). Loch Rannoch planktivorous, benthivorous and Ericht piscivorous were most successfully allocated to their a priori groupings with 87.5, 90.3 and 92.3% of fish being correctly allocated respectively. Notably, no L. Rannoch piscivores were misclassified as L. Ericht piscivores with only one L. Ericht piscivore being misclassified as a L. Rannoch piscivore. Similarly, no L. Rannoch planktivores were misclassified as L. Ericht planktivores and only one L. Ericht planktivore was misclassified as a L. Rannoch planktivore. Loch Tay fish were most commonly misclassified as L. Ericht planktivores (13 fish) but were also misclassified as L. Rannoch benthivores, planktivores and piscivores, and L. Ericht piscivores (3, 2, 1 and 1 fish respectively).

Table 4.2 Means of size corrected morphometric variables for each group. (Abbreviations as in chapters 2 and 3).

	HDO	HDE	HL	MAX	BJ	EYE	FIN	JW	SC
Tay ^{1}	38.40^{4}	27.39^{4}	44.64	20.62^{3}	25.11	10.38^{46}	35.64	11.45^{5}	1.16^{24}
Rannoch piscivorous ^{2}	39.86^{435}	28.76^{345}	48.76^{1345}	23.29^{1345}	30.19^{1345}	11.16^{13456}	37.71	17.72^{13456}	1.10
Rannoch benthivorous ^{3}	36.88	27.34^{4}	45.48^{4}	18.72	25.04	10.44^{46}	35.04^{246}	16.27^{1456}	1.14^{24}
Rannoch planktivorous ^{4}	36.15	25.57	42.04	20.10	26.06	9.50	37.31	13.52^{15}	1.08
Ericht planktivorous^{5}	36.93	26.35	43.23	19.51	24.12	10.02 6	36.39	9.62	1.18^{234}
Ericht piscivorous ^{6}	38.27	29.15^{1345}	51.74^{12345}	24.52^{1345}	28.99^{1345}	9.11	37.28	13.19^{15}	1.15^{24}

Superscripts indicate groups which are significantly different at $p<0.05$

Table 4.3 Contributions of the size corrected morphometric variables to PC1-PC4. Abbreviations as in chapter 2 and 3.

variable	PC1	PC2	PC3	PC4
HDO	-0.338	-0.273	0.138	0.094
HDE	-0.421	-0.269	0.109	-0.040
HL	-0.404	-0.103	-0.025	-0.311
MAX	-0.423	-0.051	-0.326	-0.121
BJ	-0.433	0.184	-0.144	-0.114
EYE	-0.239	-0.003	0.527	0.705
FIN	-0.280	0.206	-0.413	0.423
JW	-0.190	0.345	0.621	-0.429
Z/X	0.083	-0.803	0.063	-0.076
% variance	45.0	14.0	12.0	8.3

Table 4.4 Mean scores ± s.e. for each charr group on PC 1-3.

	PC1	PC2	PC3
	mean± s.e.	mean± s.e.	mean± s.e.
Tay ^{1}	0.3013± 0.326	-0.6823± 0.152 ^{234}	-0.1422± 0.088 ^{23}
Rannoch piscivorous ^{2}	-2.221± 0.309 ^{1345}	0.6985± 0.133	0.6529± 0.159
Rannoch benthivorous ^{3}	0.4199± 0.206	0.1517± 0.152 ^{4}	0.9390± 0.094
Rannoch planktivorous ^{4}	0.8813± 0.275	1.1459± 0.089	-0.6481± 0.124 ^{123}
Ericht planktivorous ^{5}	1.1814± 0.197	-0.7739± 0.127 ^{234}	-0.6656± 0.0938 ^{123}
Ericht piscivorous ^{6}	-1.5794± 0.286 ^{1345}	-0.4844± 0.110 ^{234}	-1.2388± 0.117 ^{12345}

Superscripts indicate groups which are significantly different at $p<0.05$

Table 4.5 Discriminant analysis of all charr groups using the 9 size corrected morphometric variables.

	Tay	Rpisc	Rben	Rplank	Eplank	Episc
Tay	22	0	1	2	3	1
Rpisc	1	28	6	0	0	0
Rben	3	2	51	2	1	1
Rplank	2	1	6	28	1	0
Eplank	13	0	2	0	30	0
Episc	1	0	0	0	0	24
N	42	31	66	32	35	26
% correct	52.4	90.3	77.3	87.5	85.7	92.3

Table 4.6 Means ± s.e. of size corrected gill raker separations and lengths and gill raker numbers for each group.

	SEPARATION	LENGTH	NUMBER
Tay ^{1}	1.246 ± 0.0342^{236}	3.4978 ± 0.115	23.90 ± 0.306
Rannoch piscivorous ^{2}	1.609 ± 0.0251	2.5607 ± 0.099^{1456}	23.74 ± 0.204
Rannoch benthivorous ^{3}	1.385 ± 0.0257^{26}	1.8845 ± 0.053^{12456}	23.15 ± 0.199
Rannoch planktivorous ^{4}	1.357 ± 0.0238^{26}	3.1784 ± 0.109	24.80 ± 0.191^{35}
Ericht planktivorous ^{5}	1.297 ± 0.0572^{26}	3.2353 ± 0.178	23.39 ± 0.458
Ericht piscivorous ^{6}	1.569 ± 0.0301	3.1987 ± 0.278	26.13 ± 0.336^{1235}

Superscripts indicate groups which are significantly different at $p<0.05$

Gill rakers

Loch Rannoch piscivorous followed by L. Rannoch benthivorous charr had the shortest gill rakers with both these groups being significantly different from each other and the other four groups ($F_{5,99}$=20.43, p<0.001; Table 4.6). Gill raker separation was largest in L. Ericht and L. Rannoch piscivorous morphs, these values being significantly larger than all other groups ($F_{5,101}$=22.46, p<0.001). The lowest value was recorded in L. Tay fish which was also significantly lower than that of Rannoch benthivores. Loch Rannoch benthivorous charr had the fewest, piscivorous intermediate numbers of and planktivorous the most gill rakers, although significant differences only existed between planktivorous and benthivorous morphs. Contrary to this, L. Ericht piscivorous charr had a high gill raker count, this being significantly higher than all other morphs apart from L. Rannoch planktivores.

4.4 Discussion

Overall trends

The results of the morphometric analysis presented here indicate that morphs of charr occupying similar trophic niches in adjacent lochs are broadly similar in terms of overall head size and shape (PC 1). In addition to this, loch specific differences were apparent (PC 2) in head shape.

Functional significance of individual traits

The functional significance of larger trophic features such as jaws, maxillary bones and overall head size, as seen in the piscivorous morphs, is clearly to enable them to capture and engulf large prey items i.e. fish, as gape size is correspondingly large (See Figs 2.1 and 3.2). Similarly, proportionally smaller heads in the L. Tay fish and L. Ericht and L. Rannoch planktivores are adaptations to a pelagic habitat where fish swim constantly to pursue plankton and therefore need to be fusiform in order to maximise swimming efficiency (Swain and Holtby, 1989) and require finer jaws to capture individual plankters. Snout roundness would, for similar reasons be expected to be lower in planktivorous morphs. This is true of L. Rannoch planktivores which have the least round (most acute) snouts in contrast to the L. Ericht planktivores which have the most rounded snouts. Loch Rannoch benthivores, which specialise on small benthic invertebrates such as *Pisidium* sp. bivalves and chironomid larvae also had small heads similar to the planktivorous forms but had significantly greater jaw widths. This adaptation is also present in the benthivorous morphs of Thingvallavatn (Malmquist, 1992). The feeding behavior of the L. Rannoch and Ericht morphs in the wild is unknown although previous studies have shown that benthic specialist Dolly Varden charr, *Salvelinus malma,* engulphed large volumes of bottom sediments which they sifted through and retained only the desired prey items (Schutz and Northcote, 1972). If such a strategy is employed by L. Rannoch benthivorous charr, then broad jaws would clearly be advantageous.

Examination of gill rakers provides strong evidence for morphology being adaptive. The three planktivorous forms (L. Tay charr and Ericht and Rannoch planktivores) had the smallest gill raker separations and amongst the longest gill rakers, properties associated with effective retention of small prey items (Lavin and Mcphail, 1986). Rannoch benthivores in contrast had the shortest and fewest gill rakers, features often observed in benthivorous species or morphs (McPhail, 1984; Sandlund *et al.*, 1992). Interestingly, gill raker counts of L. Ericht piscivores were higher than L. Ericht planktivores, as with PC2 this feature differs on a geographical (inter lake) level rather than a morph level.

Role of competition and niche availability in evolution of polymorphisms

The most direct evidence for the mechanism whereby sympatric speciation occurrs has been provided by Schluter (1994). His study examined the growth of individuals of a stickleback population exhibiting a range of trophic morphology in the presence and absence of sticklebacks exhibiting limnetic trophic morphology. In the absence of limnetic competitors, growth was not associated with any particular trophic morphology. In the presence of limnetics, however, of the original population, growth was most reduced in individuals exhibiting similar morphologies to the limnetics and least reduced in morphologically least similar (more benthic-like) individuals. Thus disproportionately high competition between phenotypically similar individuals is likely to favour morphologically distant individuals and hence character release.

Other factors thought to be responsible for the promotion of trophic divergence are significant habitat heterogeneity and the absence of other fish species, in other words, the presence of vacant niches (Snorasson *et al*, 1989). Strong evidence for this is provided by Lindsey (1981) who demonstrates that individuals of *Coregonus* sp. only diverge into specialist benthivores and planktivores (characterised by low or high gill raker counts respectively) in the absence of *Prosopium* sp. which are more specialised benthivores (low gill raker counts) and the ciscoe *Leucichthys* sp., a more specialised planktivore (high gill raker counts). Similarly, in the absence of coregonids *Prosopium* populations are observed to exhibit polymorphism with morphs exhibiting gill raker counts in the range that would otherwise be occupied by Coregonids. In this study L. Tay charr were observed to have the longest and least separated gill rakers and a head morphology and colouration typical of a planktivorous feeding morph, thus they may be more specialised for plankton feeding than the L. Rannoch and Ericht planktivorous morphs. Thus, it is possible that L. Tay charr are somehow excluded from utilising benthic resources more fully, which is reflected in their morphology. There is indirect but convincing evidence that such a scenario exists. Approximately 25% of charr retrieved from gill nets in L. Tay showed signs characteristic of attack by eels *Anguilla anguilla*: this was rarely if ever the case in the other two lochs. That Loch Tay has a substantial, eel population in relation to the other lochs is entirely likely given that migratory eels and salmonids have direct access to L. Tay from the sea in contrast to the other two lochs which are at higher altitudes and are virtually (L. Rannoch) or completely (L. Ericht) innacessable to migratory salmonids. It is therefore proposed that eels occupy the benthic niche in L. Tay preventing character release. It should, however, be noted that out of 42 L. Tay charr caught during the summer, whilst almost all fish were found to contain high numbers of cladocerans, two fish contained benthic prey items, one of which also contained fish remains and neither of which contained cladocera. These fish exhibited atypical pale colouration and morphometric analysis indicated that they possessed morphologies which were at the extreme range of the morphological variation of L. Tay charr (see Fig. 4.2). These were the only individuals found to exhibit such morphologies out of approximately 150 charr examined from L. Tay, thus no firm conclusions can be made regarding the basis for this variation. Certainly the morphological differences were less pronounced than in the L. Rannoch and Ericht morphs which suggest that these differences may be due to long term foraging and habitat specialisations (Day *et al.*, 1994; Curtis *et al.*, 1995; Knudsen, 1995; Knudsen *et al.*, 1996; Bourke *et al.*, 1997) which induce phenotypic change. Alternatively these fish may represent a true benthic morph which is present at very low density.

Role of loch bathymetry in evolution of polymorphisms

While the L. Rannoch benthivorous form has a discrete spawning site at the mouth of the afferent River Gaur, (Adams *et al.*, in press), a feature which in itself would allow for reproductive isolation, the fact that this form is found only in the west basin into which the R. Gaur flows, outwith the spawning period as well (Chapter 6) indicates that the shallow constriction between the two basins may aid in the isolation of the benthivorous and piscivorous morphs (Fig 4.3). These forms are therefore segregated both trophically and micro-allopatrically. The trophic differences in these two forms possibly reflects different feeding opportunities in the two basins. The fact that the loch's populations of pike *Esox lucius* and perch *Perca fluviatilis* are almost exclusively located in the west basin (chapter 6) further suggest that large habitat differences exist between the basins. Both L. Ericht and Tay are comprised of a single basin thus show no such segregation. A

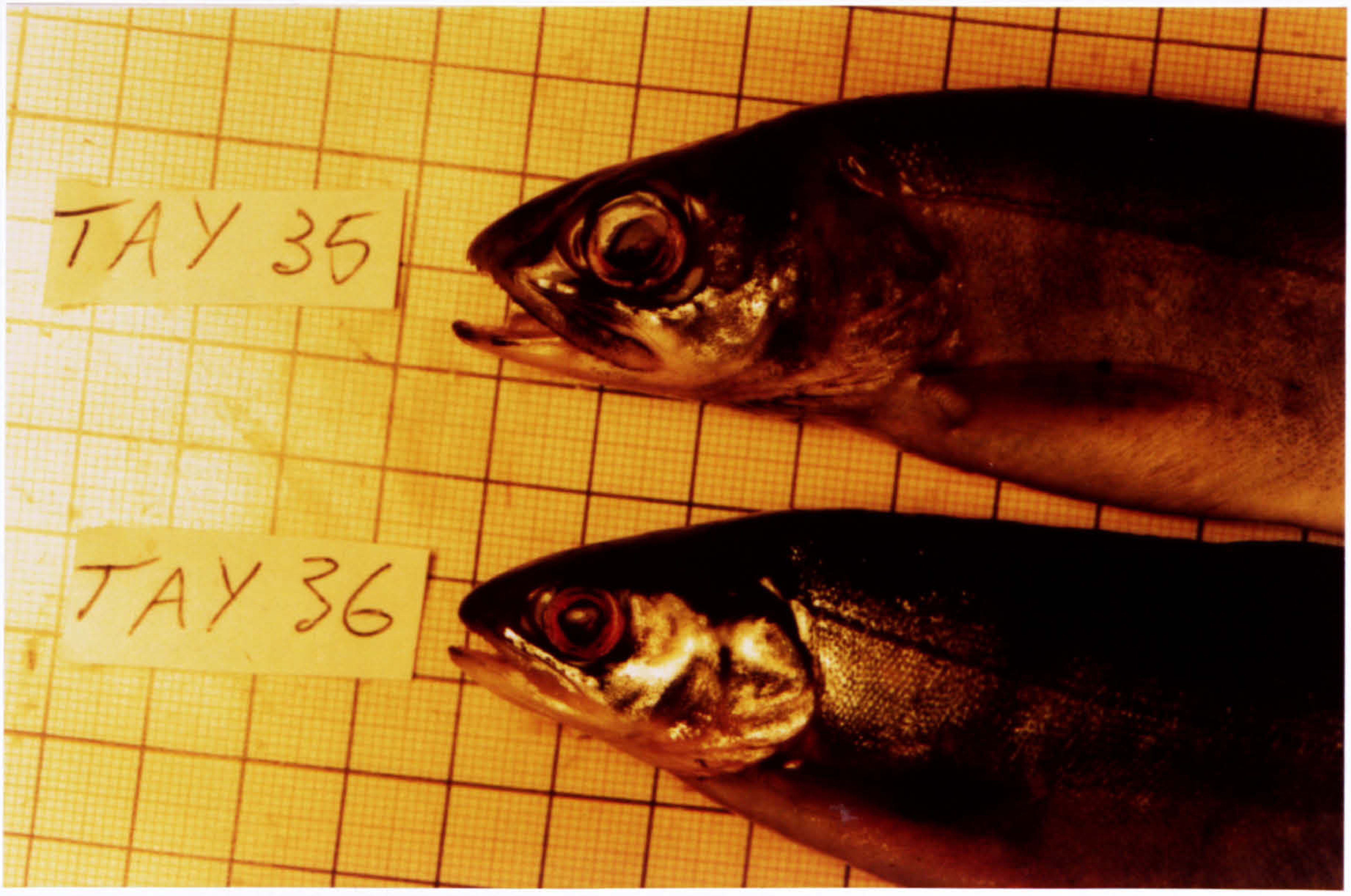

Figure 4.2 Two Arctic charr from L. Tay. The bottom fish was brightly coloured with a small head and eye, contained zooplankton and typified the population as a whole. The top fish exhibited pale colouration, had a relatively large head and eye despite being of similar size, and contained benthic invertebrates and fish remains.

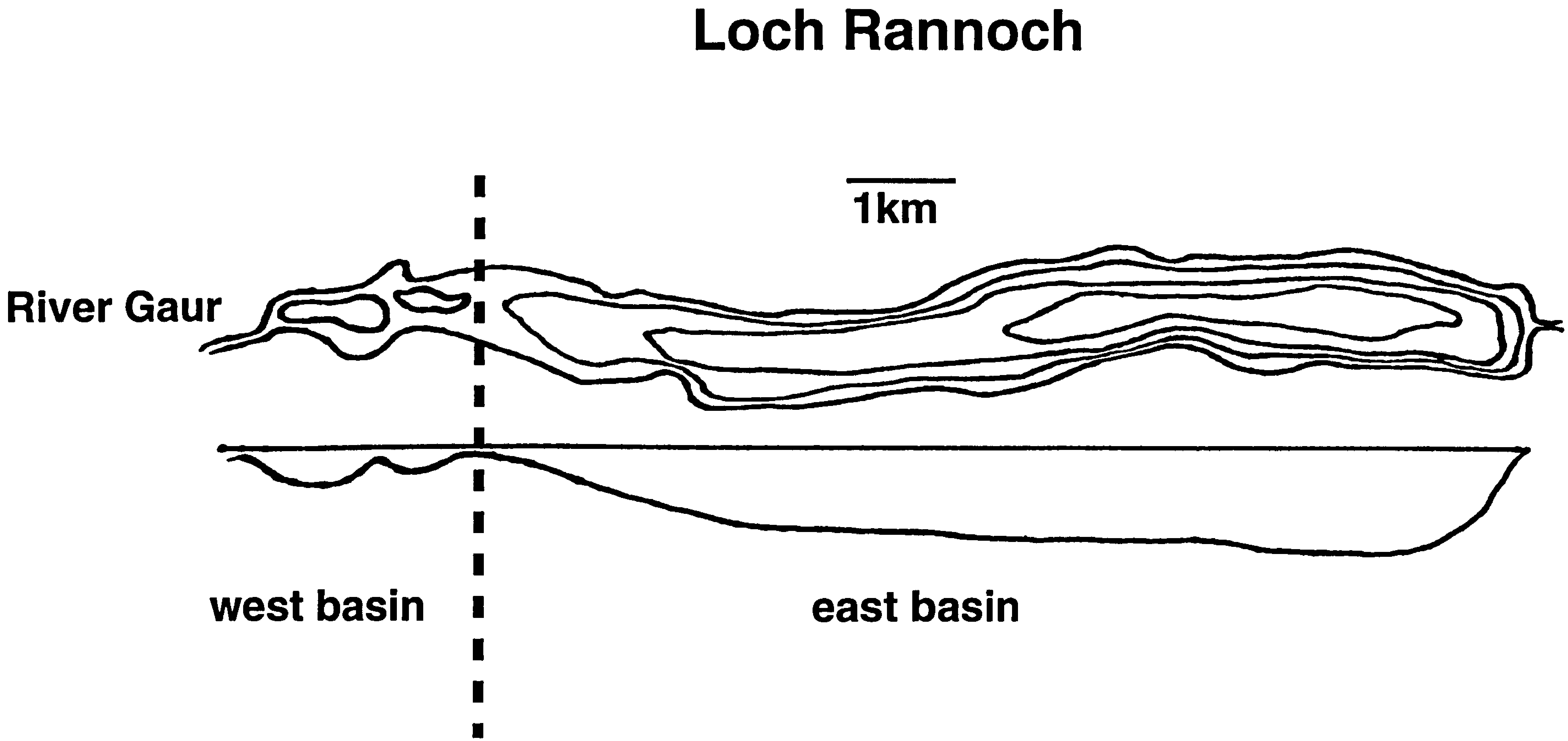

Figure 4.3 Map (top) and longitudinal bathymetric profile (bottom) of L. Rannoch showing the discreteness of the two basins.

similar effect of lake bathymetry is found in Lake Windermere where autumn and spring spawning races are further segregated into north and south basin races although no trophic basis exists for this differentiation (Partington and Mills, 1988).

In addition to L. Ericht and L. Rannoch piscivores showing close morphometric similarities, comparisons of growth patterns between Rannoch planktivores and piscivores and Ericht planktivores and piscivores indicate that close life history parallels exist (chapters 2 and 3). Other instances of the existence of an additional morph to a benthivorous and a planktivorous morph involve unusual niches existing, for example the interstitial space in the volcanic substrata of Thingvallavatn which is utilised by the small benthivorous morph which is one of three genetically distinct spawning populations in the lake (Sandlund *et al.*, 1992).

Allopatric versus sympatric speciation hypothesies

It is not clear why some lakes e.g. L. Ericht should show dimorphism while other apparently similar lakes e.g. L. Tay should not. This anomaly possibly supports the contention that dimorphism requires the invasion of two allopatrically derived charr populations and that L. Tay did not receive these. Genetic analysis of two of the three L. Rannoch morphs (benthivorous and planktivorous) by Hartley *et al.* (1992) suggests that these two forms represent invasions of two allopatrically derived races (see chapter 9 for further discussion of this issue).

In addition to the experimental work carried out on threspined sticklebacks which indicate that sympatric speciation has resulted in the existance of trophic morphs of sticklebacks (Schluter, 1993;1994; Rundle and Schluter, 1988) other studies attempting to determine the systematics of sympatric morphs by molecular genetic means have provided strong evidence for sympatric speciation. Taylor *et al.* (1996) demonstrated that two forms of sockeye salmon *Oncorhynchus nerka,* the anadromous form and the freshwater resident (kokanee) form had arisen repeatedly and independently throughout its range after initial postglacial colonisation, although superimposed on this was evidence for two broad geographical groups derived in allopatry. Similarly Hindar *et al.* (1996) demonstrated that comparable charr morphs in different Norwegian lakes were less genetically similar than morphs within the same lake indicating that morphs have evolved sympatrically within lakes. Furthermore, Volpe and Ferguson (1996) determined that limnetic charr from Thingvalavatn were more similar to sympatric small benthivorous charr than to limnetic charr from other Icelandic lakes. Further genetic studies of the charr populations in the three lakes described could lead to a better understanding of their evolutionary relationships.

CHAPTER 5 - LIFE HISTORY STRATEGIES AND REPRODUCTIVE INVESTMENT IN ARCTIC CHARR IN LOCH RANNOCH.

5.1 Introduction

In addition to morphological adaptations to various habitats and environmental conditions amongst differing water bodies, populations of Arctic charr also show great variations in life history traits. These include growth rates, size and age at sexual maturity, spawning frequency and the degree of reproductive investment. Thus, anadromous (sea-going) populations typically differ from freshwater resident populations in that they mature at a relatively advanced age, live longer, grow to a large size and spawn relatively infrequently (Dutil, 1986; Johnson, 1980; Tallman *et al.*, 1996). In addition to such between-population variation, a number of studies have determined the existence of more than one form of Arctic charr within a single water body. Some of these multiple forms appear to be a consequence of different life history strategies or developmental routes resulting in, for example, resident "dwarf", resident "normal" or anadromous individuals derived from a single parental morphotype (Nordeng, 1983) or the "dwarf and "normal" forms thought to arise due to different feeding opportunities (described by Hindar and Jonsson, (1993)). However, others appear to represent reproductively isolated sympatric populations, most notably the four morphs occurring in Thingvallavatn in Iceland (Sandlund *et al.*, 1992) or the "dwarf" and "normal" forms described by Svedäng (1990).

Adams *et al.*, (in press) describe the occurrence of three morphologically and ecologically distinct populations of Arctic charr from Loch Rannoch, Scotland. The three forms are: i) a piscivorous form (exhibiting pale colouration and retaining parr marks into adulthood) which occurs epibenthically at depths greater than 15m and consumes benthic invertebrates until a critical length of approximately 16cm is reached, whereafter it preys on other fish, ii) a benthivorous form with similar colouration, but with differing head morphology which feeds entirely on benthic macro-invertebrates throughout its size range and iii) a planktivorous form which is highly coloured and occurs throughout the lake in the pelagic zone and feeds on zooplankton. Spatial differences in spawning site (Adams *et al.*, 1998) amongst the three morphs and genetic polymorphism at the mtDNA HIND*i* III locus in two of the three morphs examined to date (benthivorous and planktivorous) (Hartley *et al.*, 1992), together with rearing experiments of the same two morphs (Adams and Huntingford, in prep), indicate that the three forms are reproductively isolated and are discrete spawning populations.

To examine if morphological and ecological differences between the morphs translate into differences between morphs in life history patterns, I compared a number of life history traits among the morphs and examined the effect these had on lifetime reproductive output of each morph.

5.2 Materials and methods

Study site

Loch Rannoch (GR. NN5957 56°41.3' 4°17.7'W42) is situated in Perthshire, Scotland (Fig 1.3) at an altitude of 203m above sea level. It is a deep, oligotrophic fjiord-like lake, with a maximum depth of 116m (Murray and Pullar, 1910) and a mean depth of 51m. A number of fish are present in the loch (see chapter 2) and although the brown trout *Salmo trutta* (L.) of the loch are subject to angling mortality, charr are not the subject of any recreational or commercial fishery.

Capture of fish

Sampling was carried out during 1994 - 1996 from October 15th to 8th November, the period during which all three populations spawn (chapter 2; Adams *et al.*, 1998). Multi-panelled gill nets (8 panels, knot to knot mesh size ranging from 8-50mm) were set at a range of depths in both the west basin, where the afferent River Gaur enters the lake (the spawning site of the benthivorous morph; chapter 1) and in the east basin, where the piscivorous morph spawns at depths of 10m or more and the planktivorous form spawns in the littoral zone at depths of 5-1m. Nets were set for periods of approximately 24h. All charr captured were removed from nets and were frozen within 6h.

Post mortem procedure

Fish were thawed in a refrigerator over approximately 24h in order to maintain tissue integrity. Fish were identified to morph level (planktivorous, piscivorous or benthivorous) on the basis of head morphometrics (chapter 2; Adams *et al.*, 1998). The following characteristics were then recorded: Fork length (to the nearest mm), fish weight, gender, reproductive status (spawning or not spawning in current season, based on the developmental status of the testis / ovaries) and testes / ovary weight. In order to determine fecundity in females, entire ovaries of each fish were immersed in modified Gilson's solution (Bagenal, 1969) for a period of approximately 2 weeks to allow them to harden; occasional vigorous shaking during this period facilitated separation of individual ova. Fecundity values were then obtained by counting every egg from each fish. Otoliths were removed for age determination. The external faces of otoliths were ground using fine (1000 grit) aluminium oxide grinding powder to increase the clarity of annuli. Annuli were counted by viewing the external face of the otoliths laterally, immersed in glycerol, illuminated from below under a compound microscope at 400x magnification.

Analysis of life history traits

Prior to regression and covariance analysis of fecundity, gonad weight, testes weight and egg weight on fork length, both axes were $\log_e$ transformed; this resulted in a linear relationship in all the above measurements. Gonado-somatic index (Gi) was calculated as the ratio of gonad weight to total fish weight excluding the gonads and the stomach contents.

Due to the size selectivity of even multiple mesh sized gill nets, smaller fish tend to be under represented in catches (Johnson, 1976; Parker and Johnson, 1991).

Age and length class distribution frequencies can therefore only be considered representative of the population at ages or lengths above the peak occurrence of age or length when all fish are equally susceptible to capture (Ricker, 1975). For the purposes of estimating reproductive output in terms of fecundity and egg mass of age classes below the age of peak occurrence, I attempted to reconstruct these age classes. This was done by back-calculating from the age of peak occurrence (capture) assuming an 85% annual survival rate from 0+ for each morph. This survival rate and technique has been is adopted for similar purposes by Jonsson *et al.*, (1984) and is based on mortality estimates by Jonsson (1977) on brown trout and Jonsson and Hindar (1982) on Arctic charr. All three populations were then standardised to 100 fish. Using the reconstructed age frequency distributions, annual population fecundity was calculated by multiplying the mean fecundity for each age group by the percentage of the overall population contained within that age group. The same calculation was carried out using mean gonad weight for each age group. Both these procedures were carried out on all three morphs separately.

5.3 Results

Age and length distribution of reproductive and non-reproductive individuals of each morph

Comparisons of age distributions amongst morphs (Fig. 5.1a-c) indicated that each differed significantly from the others (Kolmogorov-Smirnov-z test, piscivorous versus benthivorous Z=4.60, piscivorous versus planktivorous Z=6.43, benthivorous versus planktivorous Z=2.39; $p<0.001$ in each case).

Males and females of the planktivorous morph (Fig 5.1a) showed identical maturation patterns, with 50% of fish maturing at age 2+. At age 3+ immature fish comprised only 4.4% of males and 6.5% of females and by 4+ all fish were reproductive in this morph. Non-reproductive planktivorous males of age 2+ had significantly lower fork lengths than reproductive 2+ males (means =155.1mm and 175.5mm respectively, t =-2.67, $p<0.05$). Low sample sizes prevented comparison of sizes between immature and mature fish in any other age group in any other morph. Benthivorous fish (Fig. 5.1b) also exhibited 50% maturation in the female 2+ age class and 100% maturation in age group 2+ males. Age groups 3+ and 4+ exhibited 100% maturation in both sexes although, unlike planktivorous fish, small numbers of non-reproductive males and females appeared at ages 5+,6+,7+ and 9+. The age class structure of the piscivorous morph (Fig. 5.1c) contrasts strongly with those of the other two morphs. The most marked difference is in the longevity of this form which showed a maximum age of 17+ as opposed to 11+ and 7+ in the benthivorous and planktivorous morphs respectively. The maturation pattern of piscivorous individuals also differed from the other two morphs in that mature 1+ females were found whereas mature males were not apparent until age 3+. Non-spawning, but presumably previously maturing individuals of both sexes were apparent in most age groups.

Statistical comparisons of the length frequency distributions (Kolmogorov-Smirnov Z test; Fig. 5.2) indicated that significant differences existed between benthivorous and planktivorous morphs ($Z=5.46$, $p<0.001$) and piscivorous and

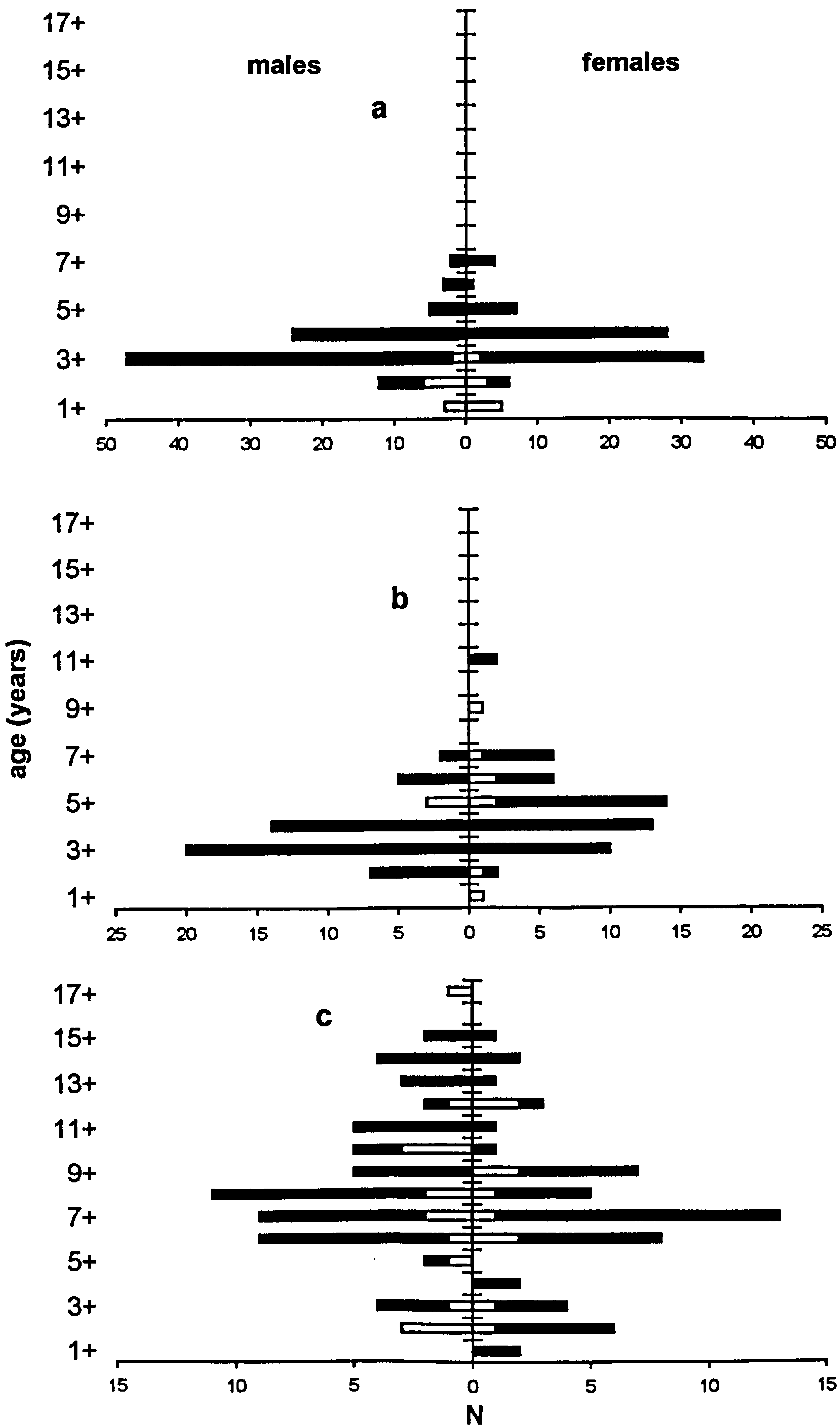

Figure 5.1 Age frequency distribution of a) planktivorous, b) benthivorous and c) piscivorous L. Rannoch charr (mature = ■ and immature = □).

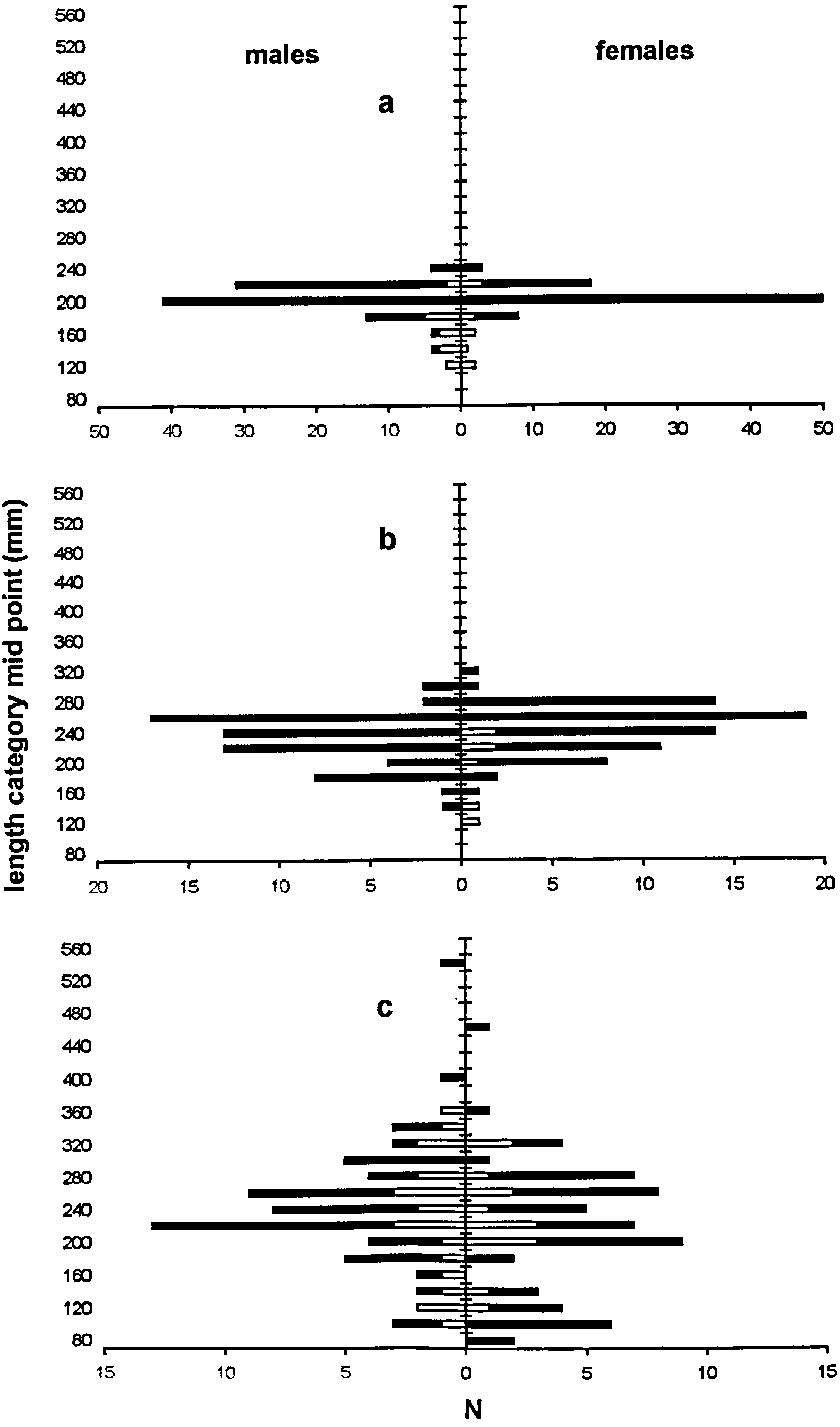

Figure 5.2 Length frequency distribution of a) planktivorous, b) benthivorous and c) piscivorous L. Rannoch charr (mature = ■, immature =□).

planktivorous morphs (Z=4.26, p<0.001), although no difference was found between piscivorous and benthivorous groups (Z=1.33, p=0.06). Spawning planktivorous fish have a very small size range (Fig. 5.2a) with males maturing at smaller sizes than females (smallest mature male = 136mm; smallest mature female = 174mm). The size range of spawning benthivorous fish (Fig 5.2b) is larger than the planktivorous fish, due to the larger sizes which the benthivorous morph attains. The smallest observed mature male (141mm) and female (167mm) are similar to the sizes of the smallest mature males and females of the planktivorous morph. Non-reproductive piscivorous fish occur at all length categories (Fig. 5.2c) with no clear relationship between size and maturation. One feature of this population is the small size at which fish were found to be reproducing, the smallest mature female being 74mm and the smallest male at 96mm.

Length at age

Differences in length at age between sexes of each morph were examined by covariance analysis of fork length on log_e age. No significant differences were found in length at age between males and females in any of the morphs, so data from males and females was pooled. Clear differences are apparent in the growth patterns of the three morphs (Fig. 5.3). The highest value of K (the Von-Bertalanffy parameter associated with growth rate; Table 5.1) was recorded for benthivorous fish (indicating that these fish have the fastest growth of the three morphs). Planktivorous fish, had the second highest K value, with the piscivorous form exhibiting the lowest growth rate with inferior mean length at age until age

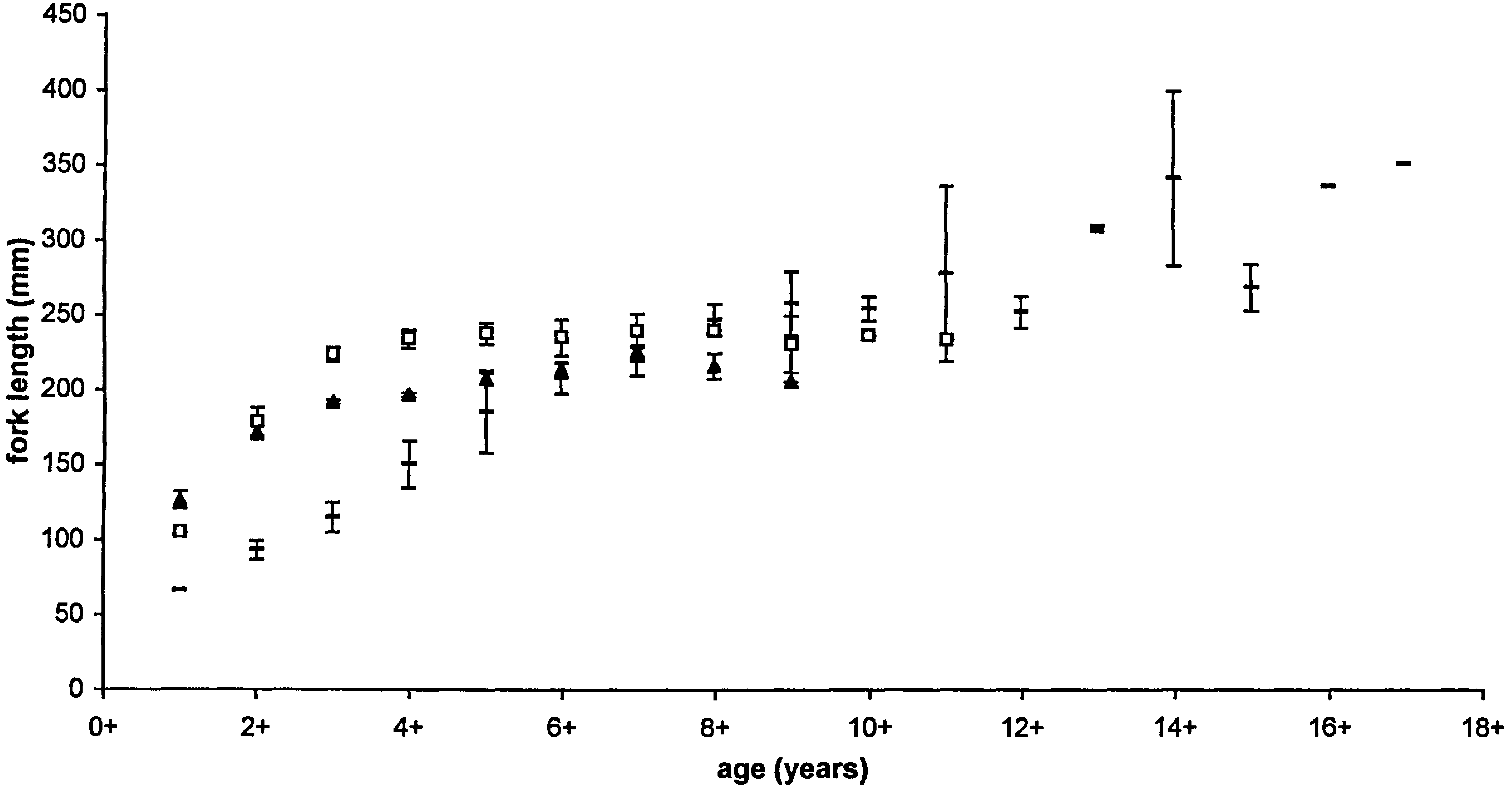

Figure 5.3 Length at age (mean ± s.e.) of each L. Rannoch charr population. (Planktivorous= ▲, piscivorous= –, benthivorous= □).

6+ when all three forms are similarly sized. A distinctive asymptote exists in the growth of both benthivorous and planktivorous forms, with almost no growth in benthivorous fish and very little growth in planktivorous fish after 3+ years. Asymptotic lengths of the growth curves (L_∞ in Table 5.1) indicate that piscivorous fish attain the greatest asymptotic length ($L_\infty = 404.1$mm), followed by

benthivorous fish ($L_\infty = 237.7$mm), with planktivorous fish exhibiting the lowest asymptotic length ($L_\infty=216.1$mm).

Relationships of fecundity, ovary weight and egg weight with fork length

The regression of fecundity on fork length was positive and highly significant for piscivorous fish (Fig. 5.4; Table 5.2; $F_{1,23}= 71.28$; $p<0.001$, R^2 75.6%). Although the same relationship was found for benthivorous fish ($F_{1,22}=9.21$; $p<0.01$), the regression accounted for a relatively small amount of the variance ($R^2=29.5\%$). No significant relationship existed between fork length and fecundity of planktivorous fish, probably due to the small size range of spawners. Covariance analysis of fecundity on fork length for benthivorous and piscivorous fish only showed a significant difference in elevations between the two forms ($F_{1,46}=45.14$; $p<0.001$), with the benthivorous form having the higher intercept (Table 5.2).

Both benthivorous ($F_{1,22}=33.29$; $p<0.001$) and piscivorous ($F_{1,25}=87.6$; $p<0.001$) groups showed highly significant positive relationships for regressions of ovary weight on fork length (Table 5.2) (R^2 =60.2% and 77.8% respectively). No significant relationship was found with the planktivorous group. Analysis of

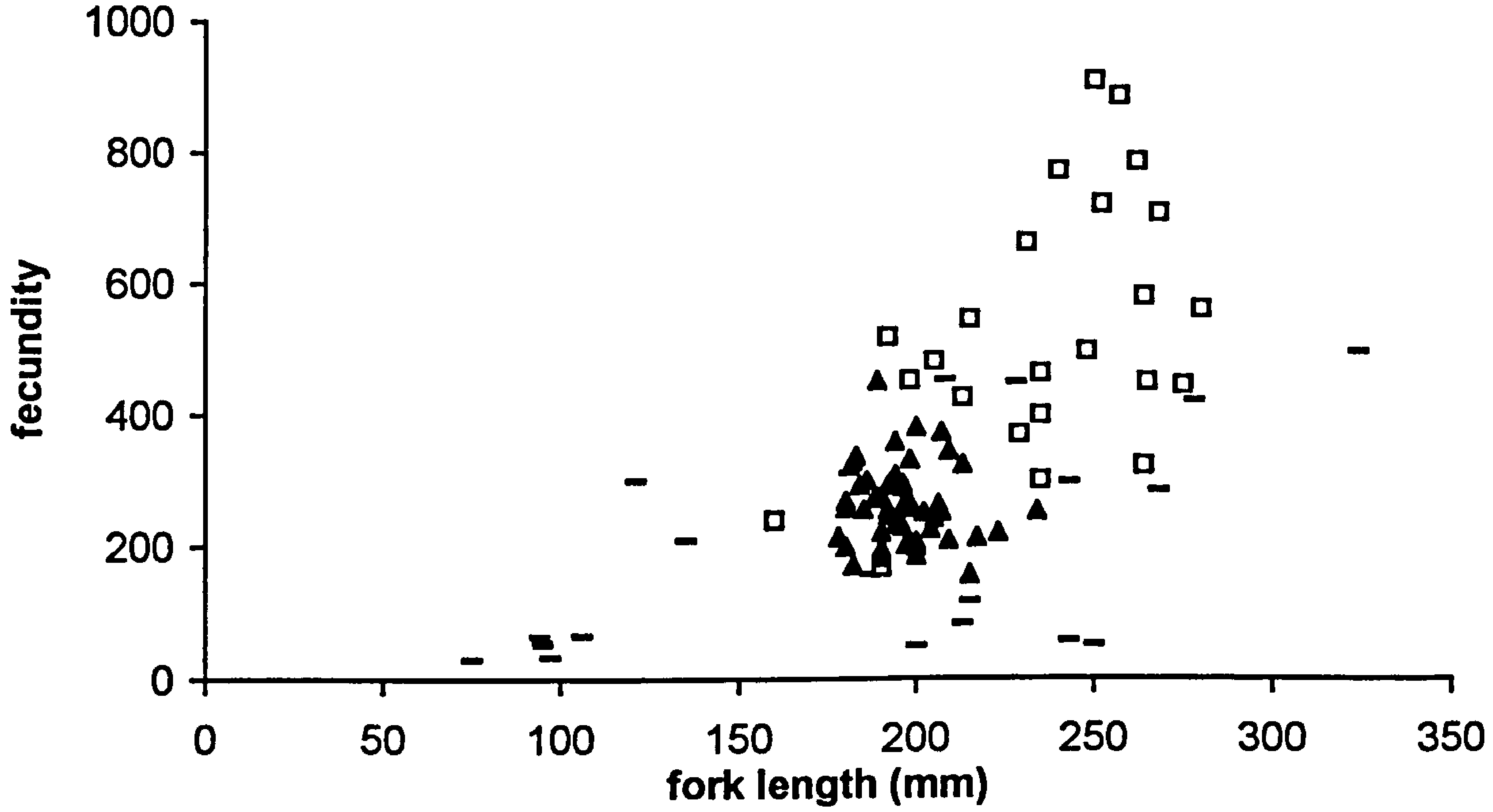

Figure 5.4 Fork length versus fecundity for each L. Rannoch charr population. (planktivorous= ▲, piscivorous= –, benthivorous= □).

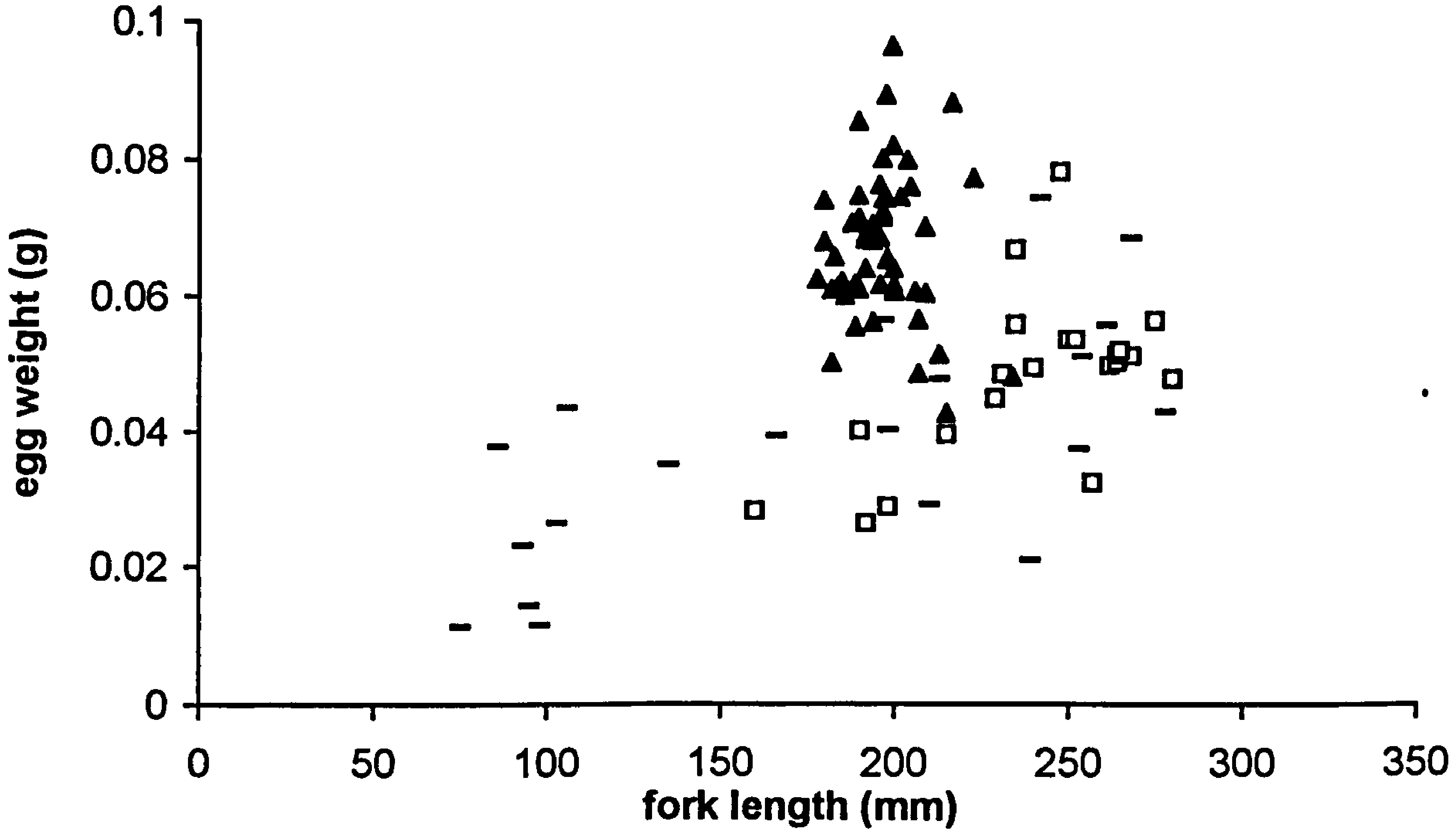

Figure 5.5 Fork length versus egg weight for each L. Rannoch charr population. (planktivorous= ▲, piscivorous= –, benthivorous= □).

covariance between piscivorous and benthivorous groups (Table 5.3) indicated a significant difference in elevation between the two groups ($F_{1,48}$=146.7; $p<0.001$) with the benthivorous group having a higher elevation (Table 5.2). Significantly positive relationships between egg weight and fork length (Table 5.2; Fig. 5.5) are shown by both benthivorous ($F_{1,19}$=15.5; $p<0.001$) and piscivorous groups ($F_{1,23}$=23.37; $p<0.001$), but not by planktivorous fish. Covariance analysis of the regressions for benthivorous and piscivorous fish (Table 5.3) showed a significant difference ($F_{1,43}$ =39.99; $p<0.001$), with piscivorous fish having a greater intercept (larger eggs) than benthivorous morph.

Given that fecundity, ovary weight and egg weight of planktivorous fish showed no significant relationship with fork length, probably due to the small size range of the spawning population, fish within the fork length range of the planktivorous population were used to examine between-morph differences in these variables. Over this size range, benthivorous fish had significantly higher fecundities and ovary weights (*post hoc* analysis by Tukey's HSD test, $F_{2,64}$=39.55;$p<0.05$; $F_{2,64}$=23.24, $p<0.05$ respectively) than both piscivorous and planktivorous fish, with planktivorous fish having significantly higher fecundities and ovary weights than piscivorous fish (Table 5.4). Planktivorous fish had significantly heavier eggs than benthivorous and piscivorous fish ($F_{2,74}$=37.88, $p<0.05$).

Table 5.1. Values of the parameters of the Von-Bertalanffy growth equation fitted to length at age data for three morphs of Arctic charr from Loch Rannoch.

parameter	benthivorous	piscivorous	planktivorous
L_∞	237.7	404.1	216.1
K	0.949	0.0976	0.635
t_0	0.398	-0.912	-0.399
r^2 (%)	98.9	94.8	96.0

L_∞ is the asymptotic length.

K is a parameter associated with growth rate.

t_0 is the intercept on the time axis at zero length.

Table 5.2. Significance of regressions of $\log_e$ fecundity, ovary weight, egg weight, Gi and testes weight on $\log_e$ fork length.

fecundity	intercept	gradient	r^2 (%)		
benthivorous	-2.53	1.6	29.5	$F_{1,22}$= 9.21	<0.01
piscivorous	-4.9	1.87	75.6	$F_{1,23}$= 71.28	<0.001
planktivorous	7.39	-0.349	0.8	$F_{1,50}$=0.42	N.S
ovary weight					
benthivorous	-13.0	2.95	60.2	$F_{1,22}$=33.29	<0.001
piscivorous	-11.7	2.54	77.8	$F_{1,25}$=87.6	<0.001
planktivorous	6.94	-0.776	3.4	$F_{1,50}$=1.74	N.S.
egg weight					
benthivorous	-10.1	1.28	44.9	$F_{1,19}$=15.5	<0.001
piscivorous	-7.37	0.782	50.4	$F_{1,23}$=23.37	<0.001
planktivorous	-1.35	-0.257	0.8	$F_{1,49}$=0.38	N.S.
Gi (female)					
benthivorous	0.136	0.000139	1.2		N.S.
piscivorous	0.178	-0.000379	14.1		N.S.
planktivorous	0.703	-0.00255	32.3	$F_{1,50}$=23.81;	<0.001
testes weight					
piscivorous	-9.8	1.97	66.8	$F_{1,9}$=18.07	<0.005
benthivorous	-12.5	2.48	27.7	$F_{1,42}$=16.08	<0.001
planktivorous	-2.4	0.715	3.1	$F_{1,71}$=2.29	N.S.

Table 5.3. Results of covariance analysis of $\log_e$ fecundity, ovary weight and egg weight on $\log_e$ fork length for piscivorous and benthivorous charr morphs from Loch Rannoch.

	gradient		elevation	
	F	p	F	p
fecundity	$F_{1,45}=0.15$	N.S.	$F_{1,46}=45.14$	<0.001
ovary wt	$F_{1,47}=0.27$	N.S.	$F_{1,48}= 146.7$	<0.001
egg wt	$F_{1,42}=0.98$	N.S.	$F_{1,43}= 39.99$	<0.001
testes wt		N.S.		N.S.

Table 5.4. Means and significances of ANOVA of fecundity, ovary wt and egg weight (females) and testes weight and Gi (males) among three morphs of Arctic charr from Loch Rannoch.

	female			male	
	fecundity	ovary wt (g)	egg wt (g)	testes wt(g)	Gi
	$F_{2,64}=39.55$	$F_{2,64}=23.24$	$F_{2,74}=37.88$	$F_{2,102}= 18.67$	$F_{2,111}=19.32$
benthivorous (1)	$462.0^{2,3}$	$19.13^{2,3}$	0.0441^{3}	2.85^{3}	0.01928^{3}
piscivorous (2)	128.0^{3}	6.25^{3}	0.0466^{3}	2.92^{3}	0.02106^{3}
planktivorous (3)	261.7	17.47	0.0671	4.09	0.0392

Superscripts indicate significant differences at 0.05 level.

Regression analysis of Gi (gonado-somatic index) on fork length indicated that only planktivorous fish showed a significant relationship, with Gi decreasing with increasing fork length ($F_{1,50} = 23.81$, $p<0.001$; Table 5.2). The overall tendency was for Gi to decrease with age (Fig. 5.6) although this relationship was again only significant in the planktivorous morph ($F_{1,49}=8.21$, $p<0.01$).

Male reproductive investment

Significant relationships existed between testes weight and fork length for piscivorous ($F_{1,9}=18.07$, $p<0.005$) and benthivorous fish ($F_{1,42}=16.08$, $p<0.001$), but not in planktivorous fish (Table 5.2; Fig. 5.7). Covariance analysis of the above regressions for piscivorous and benthivorous fish showed no significant differences in either regression gradient or elevation (Table 5.3). Comparisons of testes weight of planktivorous, with benthivorous and piscivorous charr were carried out by means of ANOVA over the size range of planktivorous fish.

Planktivorous fish had significantly heavier testes than either piscivorous or benthivorous fish (Tukey's HSD test, $F_{2,102}=18.67$, $p<0.05$; Table 5.4). Male Gi was not significantly related to fork length or age in any morph and differences between morphs were therefore examined by ANOVA (Tukey's HSD test), the results of which are shown in Table 5.4. Planktivorous fish had significantly higher Gi values than piscivorous and benthivorous fish ($F_{2,124}=54.86$, $p<0.05$).

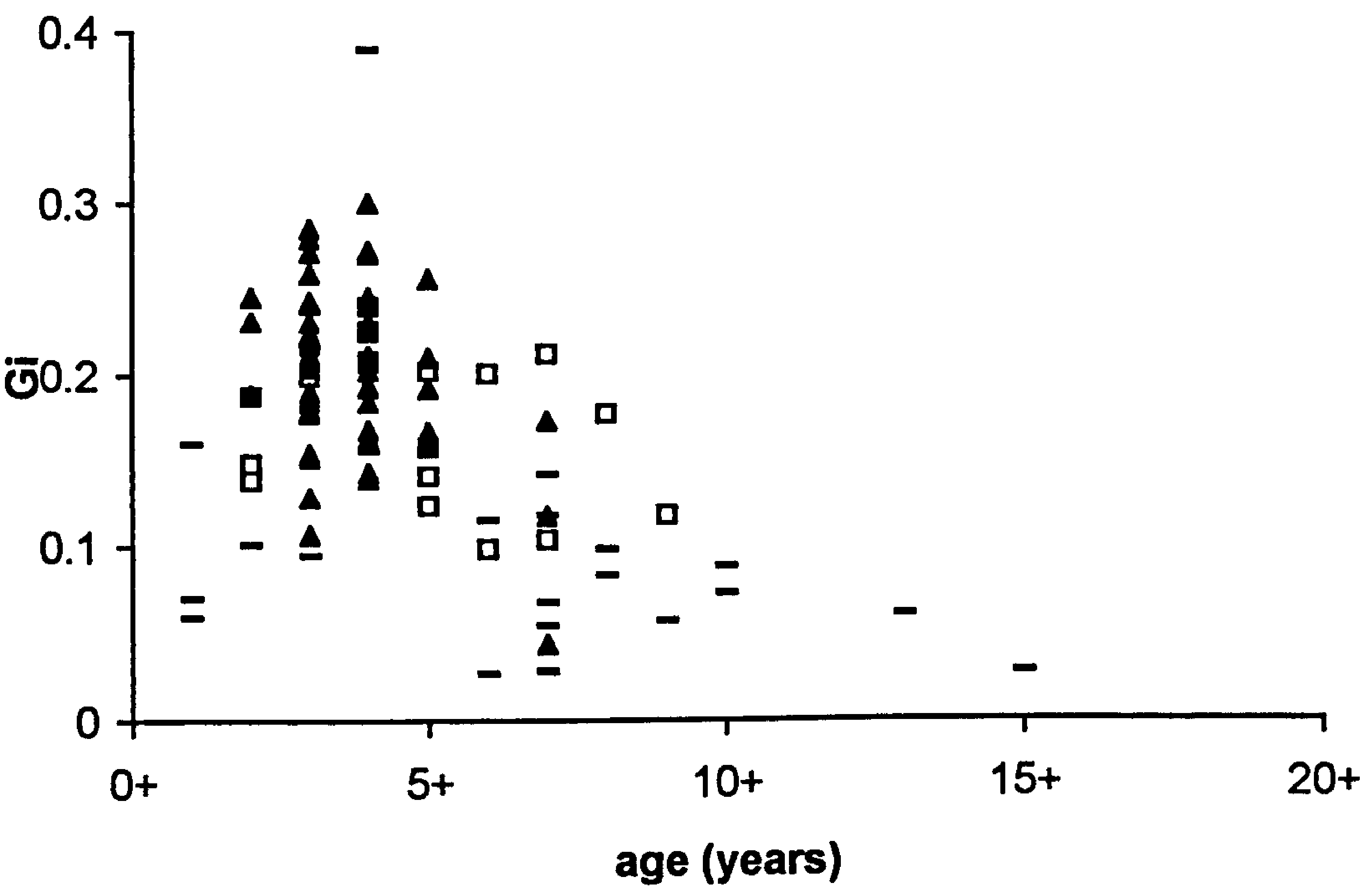

Figure 5.6 Fork length versus female Gonado-somatic index (Gi) for each L. Rannoch charr population. (planktivorous= ▲, piscivorous= –, benthivorous= □).

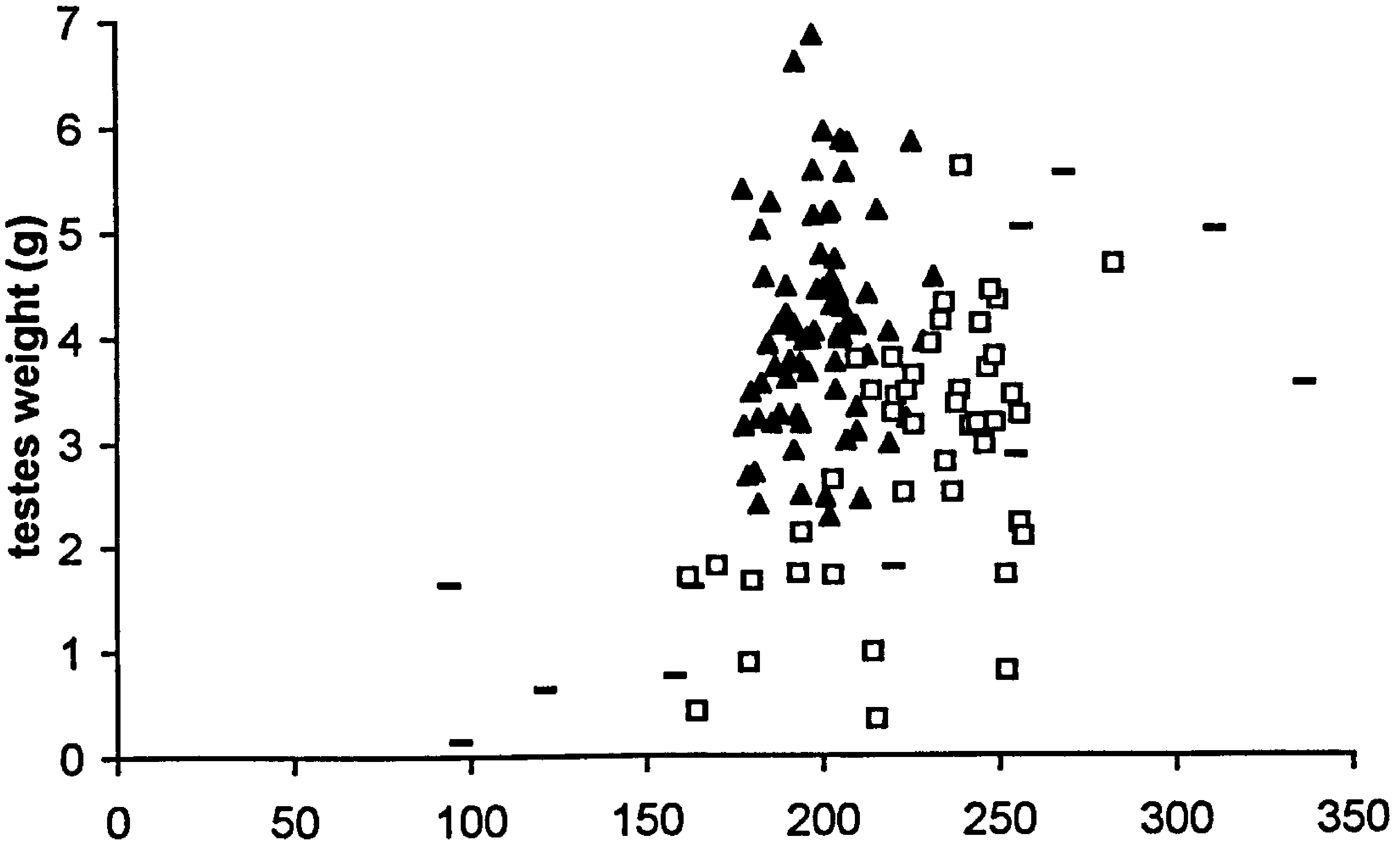

Figure 5.7 Fork length versus testes weight for each L. Rannoch charr population. (planktivorous= ▲, piscivorous= –, benthivorous= □).

Lifetime reproductive output

Fish of age 3+ contribute the most eggs to the overall population fecundity of planktivorous charr (Fig 5.8a), contributing 29.4% of the total. Fish aged 2+ and 4+ are the next most significant contributors with ages 5+ to 7+ contributing little. Fish aged 4+ followed by 3+ and 5+ are the greatest contributors to overall fecundity in the benthivorous morph, these three age classes contributing to 71% of the total. Years 2+, 6+ and 7+ are the next most important years with fish aged 8+, 9+ and 11+ contributing relatively little. The age group that produces the most eggs in the piscivorous charr population is 7+ (15.5% of total), with ages 4+ to 9+ accounting for 76.4% of the total egg production. The relative mass of eggs produced by each age group of a population of 100 fish of each morph (Fig. 5.8b) follows a similar pattern to Fig. 5.8a

The relative reproductive output (eggs produced per 100 reproducing females) is highest in the benthivorous morph, intermediate in the planktivorous morph which produces 40.2% of benthivorous output and lowest in the piscivorous morph producing 35.4% of the benthivorous output (Fig. 5.9). However, the differences between planktivorous and benthivorous populations total egg mass output is reduced due to planktivorous fish producing heavier eggs than the benthivorous morph. It is interesting to note that while age 3+ contribute the most to the fecundity of the planktivorous population, age 2+ contribute the most in terms of egg mass.

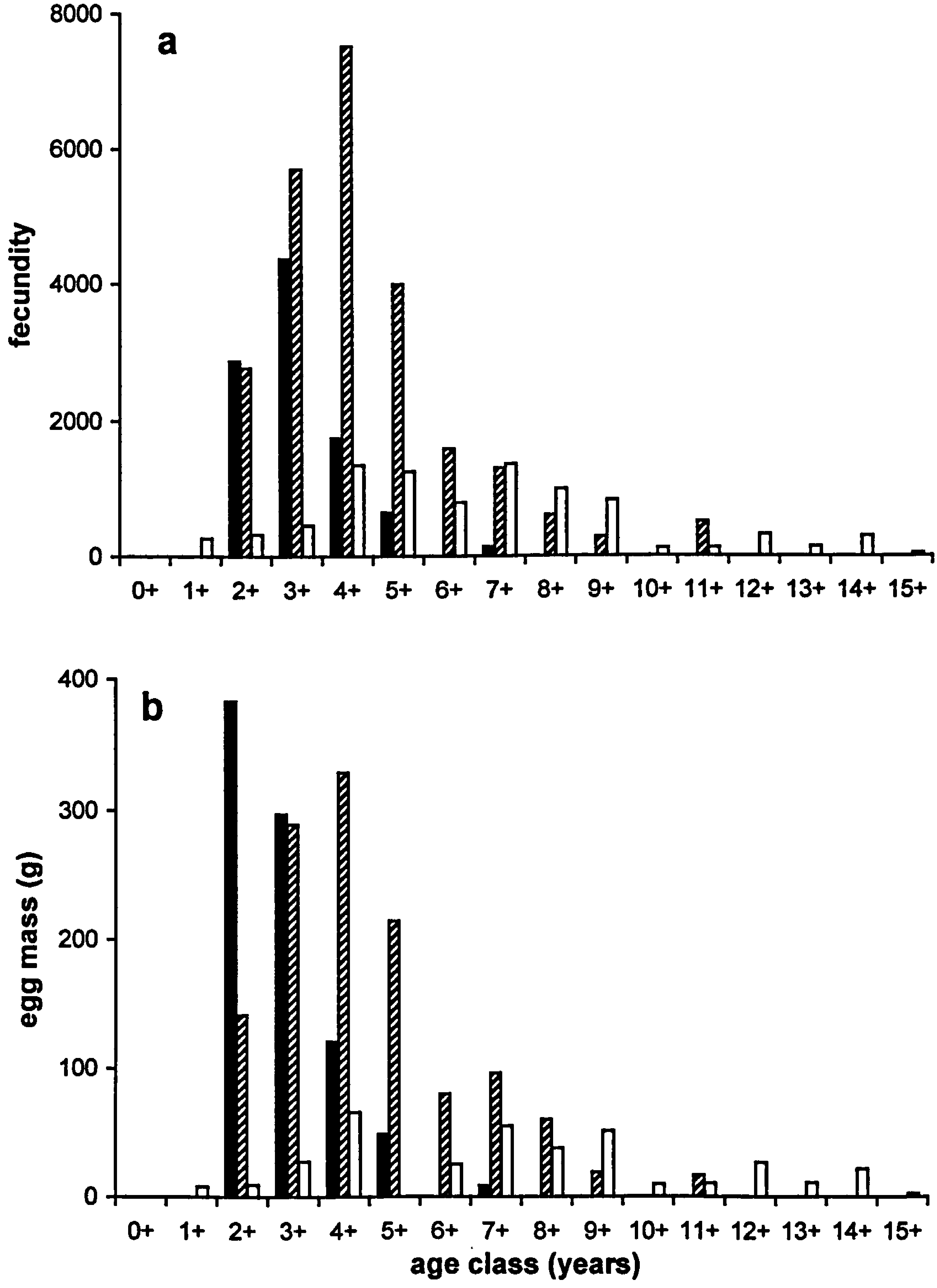

Figure 5.8 a) Relative contribution of each age class to the overall fecundity of 100 reproducing females. Values are derived by multiplying the mean fecundity of each age group by the proportion of fish contained within each age group. b) as a) exept using egg mass. (planktivorous = ■, piscivorous = □, benthivorous = stippled bars).

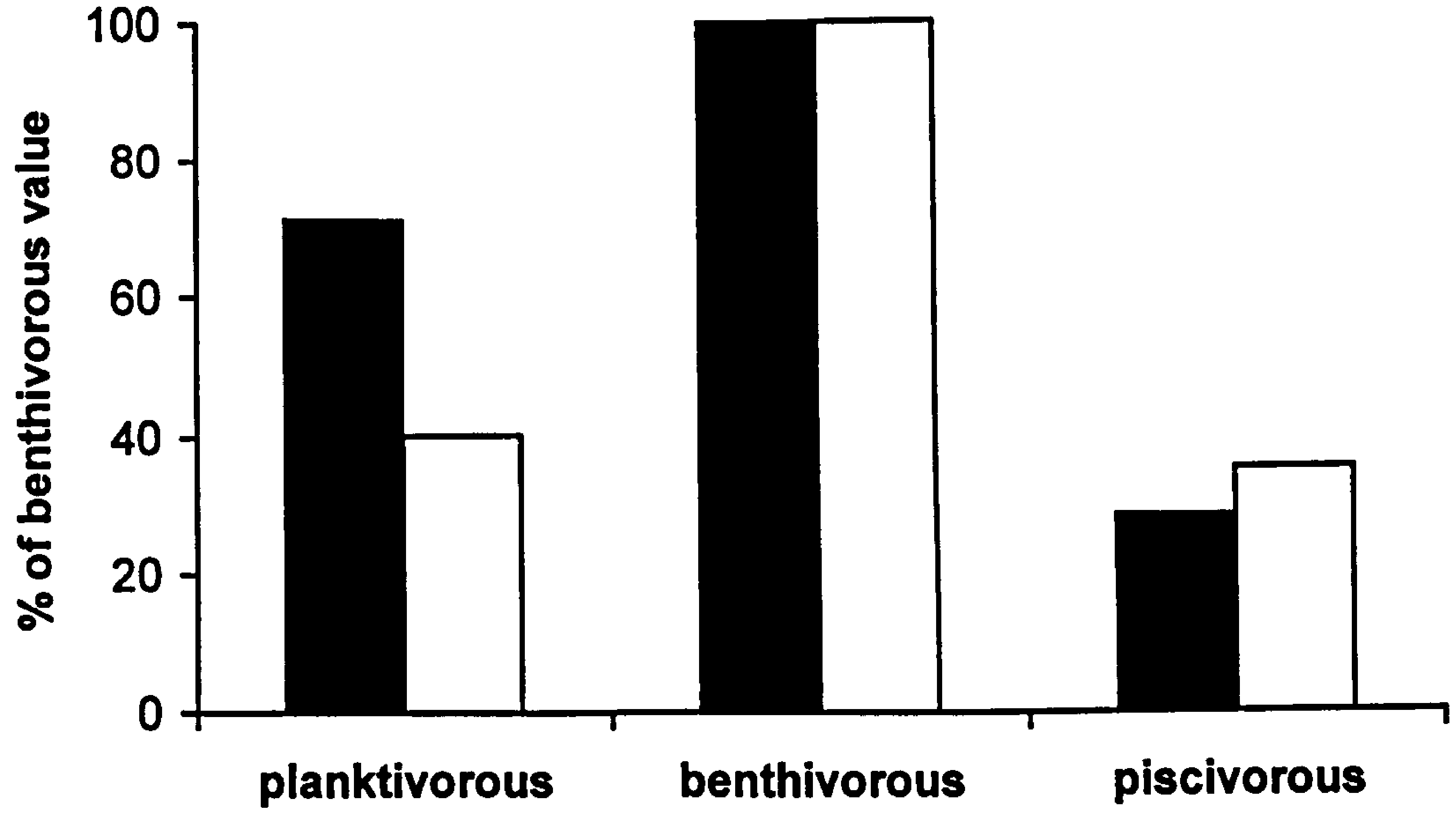

Figure 5.9 Comparative fecundity and egg mas output of 100 reproductive females (age group values from Fig. 8 summed) ■ = egg mass, □ = fecundity.

Assuming that most eggs found in the body cavity prior to ovulation are actually oviposited, mortality is highest in all three populations in the period between oviposition and the end of the first year of life (0+). Thus, planktivorous, benthivorous and piscivorous charr experience 99.13%, 99.68% and 99.12% mortality respectively at this stage (Fig. 5.10).

5.4 Discussion

As well as being discrete in terms of morphology, spawning location (chapter 2; Adams *et al.*, 1998) and genetics (Hartley *et al.*, 1992), the data presented here indicates that the three morphs of Loch Rannoch charr, also differ greatly in a number of life history traits.

Age and size at maturation

Loch Rannoch benthivorous and planktivorous charr mature at ages typical of other populations in the British Isles (Maitland *et al.*, 1984). These ages are however young compared with more northern freshwater resident charr populations which have been recorded maturing at ages very much older than this and rarely younger than 3+ (Johnson, 1980; Tallman *et al.*, 1996). Piscivorous charr are unusual in that females are reproducing at age 1+ which corresponds to a length of 74-120mm. Maturity in female salmonids at this size is a feature of some "dwarf" Arctic charr populations which although spawning at small sizes, tend to be relatively old e.g. Jonsson *et al.* (1988), Sandlund *et al.* (1992). In this study the smallest mature female (74mm) contained only 18 eggs, similar to a value of 12 eggs in a small benthivorous individual of 75mm from Thingvallavatn

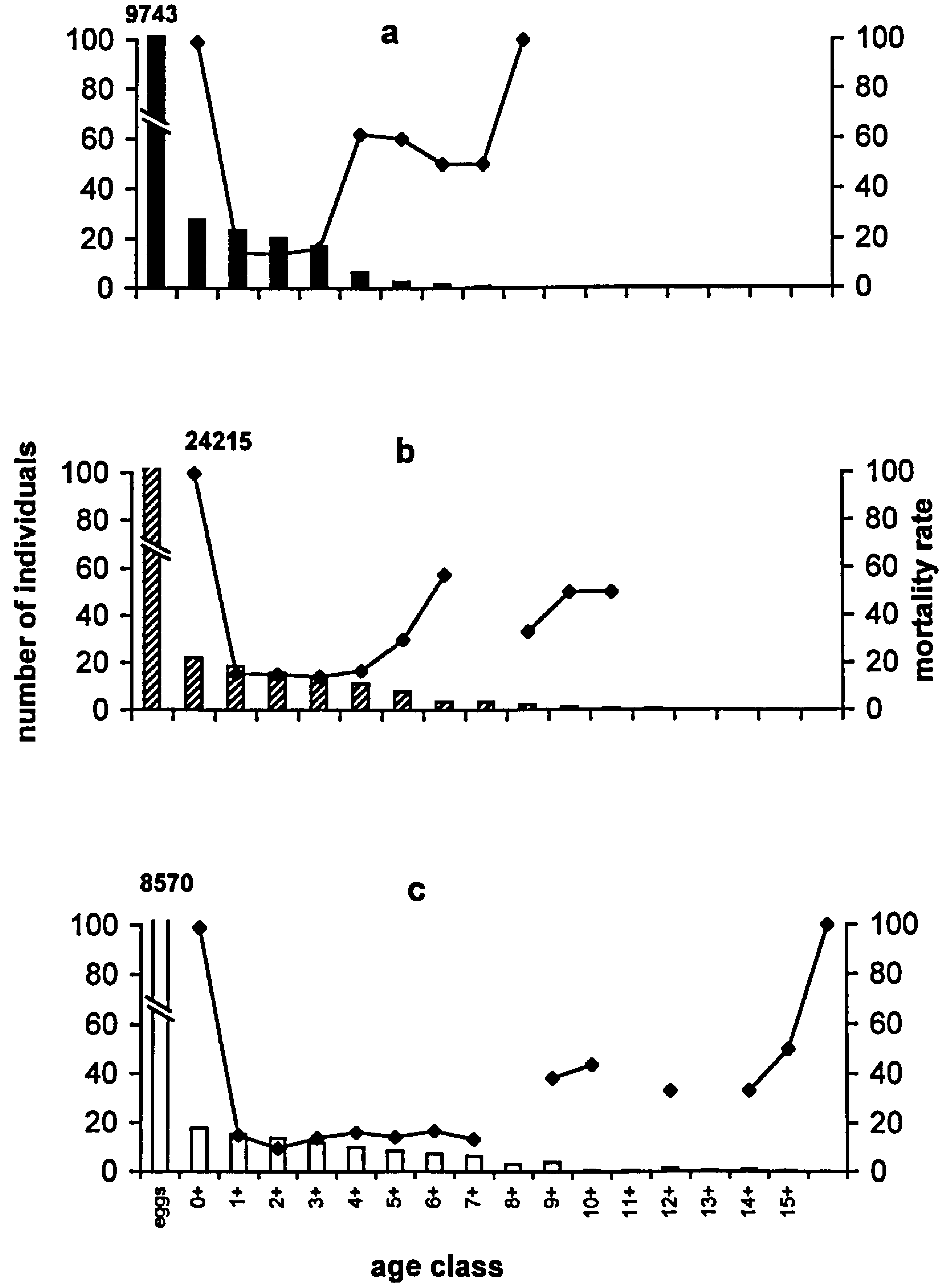

Figure 5.10 Total annual fecundity (potential egg ovipostion, as shown in Fig. 5.9) with the reconstructed age frequency distributions from which they were derived (bars) and mortality rates for a) planktivorous, b) benthivorous and c) piscivorous populations.

(Sandlund *et al.*, 1992). Although male piscivorous charr are observed maturing first at 3+ it is likely that they too matured at ages prior to this although low catches (three male fish aged 2+ and none aged 1+) prevented this from being ascertained.

Several studies have demonstrated that within a single fish species fast growth is associated with earlier maturation e.g. Alm (1959); Thorpe & Morgan (1980) and Thorpe *et al.* (1983) on Atlantic salmon; Adams and Huntingford (1997) on Arctic charr. This appears to be the case within a single morph of charr with first time spawning 2+ planktivorous males being significantly larger than juvenile, non-maturing 2+ males. If the same process operated in the piscivorous morph then given its slower initial growth rate, it would be expected to mature at a more advanced age. The fact that the piscivorous morph matures at a younger age and smaller size than either of the other two morphs indicates that these differences are largely due to genetic rather than environmental differences (growth rates). Skúlason *et al.* (1996) similarly found that progeny of the four morphs of charr in Thingvallavatn when reared under identical conditions in the laboratory showed similar maturation and growth patterns to those found in the wild. In their study the small benthivorous and planktivorous morphs although the slowest growing, were the earliest to mature, while within each morph the fastest growing or largest individuals were the first to mature. This indicated that inter morph differences were largely genetically determined. Vøllestad and L'Abée-Lund (1994) on analysing 44 populations of Arctic charr from throughout its range demonstrated a significantly positive relationship between length at maturity and asymptotic length i.e fish matured at a constant length relative to maximum size which they attain. In this respect piscivorous fish are completely anomalous as they mature at the earliest and attain the greatest sizes.

Several authors (e.g. Nordeng, 1961; Skreslet, 1973) have shown that a dietary switch to piscivory or anadromy and the associated increase in growth rate, cause fish to suspend maturation, or mature at an older age. This could possibly explain the spawning intervals and early maturation in the piscivorous morph, in that fish may be adopting a dwarf maturation strategy at small sizes, followed by periods of reproductive dormancy associated with rapid growth and piscivory. It should however be noted that non-reproductive individuals were also present at sizes below which piscivory is likely to have commenced.

Benthivorous and piscivorous morphs appear to exhibit two different strategies of reproductive investment. Piscivorous fish invest lower levels of energy in gametes by spawning less frequently and producing fewer eggs at each spawning. They do, however, continue to grow throughout their lives. Benthivorous fish invest higher levels of energy in gametes by spawning more frequently and investing in higher numbers of (similarly sized) eggs They do not, however exhibit any significant growth after maturation. Selection for sustained growth and attainment of large size in piscivorous fish operates to allow them to exploit smaller fish as prey It is hard however to reconcile this with the observation that piscivorous fish, rather than investing all their energy into growth at an early age to a) escape the risk of predation which they are subject to at smaller sizes from larger piscivorous charr (unpublished data), b) attain a size where they can adopt piscivory, are instead investing resources in reproduction.

Effects of habitat and diet on life history

Piscivorous brown trout which inhabit the loch (Campbell, 1979 (Hegge *et al.*, 1989). are known to utilise the pelagic zones of lakes and feed predominantly on planktivorous charr (L'Abee-Lund *et al.*, 1992; Campbell, 1979). The vulnerability of (planktivorous) fish in the pelagic zone is also higher than in the epibenthic zone due to its unstructured nature as opposed to the structured nature of the epibenthic zone which offers refugia for fish therein (Crowder and Cooper, 1982). L'Abee Lund *et al.*, (1993) demonstrated that charr will grow to a minimum size before utilising the pelagic habitat to avoid predation by larger brown trout therein. Habitat specific predation risk may thus explain differences in length at maturity. Higher predation risk in the pelagic zone relative to the epibenthic zone results in larger observed length at maturity in the planktivorous relative to piscivorous morph due to stronger selection for attaining a size at which predation risk will be reduced. The benthivorous morph, although utilising the structured epibenthic habitat, occurs only in an isolated basin of the loch in which pike *Esox lucius* are locally abundant (chapter 6). Predation from pike may also operate as a selective force for larger size at maturation in this population.

The different diets of the three forms are likely to have strong implications for their growth and longevity. Planktivorous and benthivorous fish are limited in growth in their latter years due to the lower foraging efficiency of larger than smaller fish of foraging on small prey items, zooplankton in the case of planktivorous fish and *Pisidium* sp and chironomid larvae in benthivorous fish (chapter 2; Adams *et al.*, 1998; Schluter, 1993; Snorrason *et al.*, 1994; Mittlebach, 1983; Hamrin and Persson, 1986). Combined with the seasonality of this resource, planktivorous fish are likely to experience higher mortality rates during the winter. Growth can however be maintained in piscivorous fish due to the switch to piscivory at approximately 16cm (chapter 6). Given that the diet of benthivorous and piscivorous charr (up to 16cm length) are almost identical, the lower length at age values observed in the piscivorous morph are likely to be due to individuals investing energy in reproduction at age 1+.

Fecundity and egg weight

The differences in fecundity and egg weight amongst the three forms are likely to be adaptations to the differing environments in which alevins will hatch out. Benthivorous charr spawn in shallow running water (approx. 2m depth) at the mouth of the afferent river Gaur. Piscivorous charr spawn sublittoraly at depths of greater than 10m while planktivorous fish spawn in the littoral zone at depths of 1-10m. Blaxter (1988) and Blaxter & Hempel (1963) have demonstred that larger yolk reserves will allow larvae of herring, *Clupea herangus* more flexibility in the timing of the switch from endogenous to exogenous feeding. Larvae will thus be more likely to survive the variable and uncertain delay from hatching until plankton becomes abundant by having larger yolk reserves. Similarly, Hutchings (1991) demonstrated that in brook charr *Salvelinus fontinalis* decreased food abundance selects for a smaller number of larger eggs as larger alevins are better able to survive periods without food. Thus larger eggs (which will have correspondingly large yolk reserves) in the planktivorous form may be an adaptation to temporal variability in the spring zooplankton bloom. Baroudy & Elliott (1994) found that Autumn spawning charr from L. Windermere had significantly larger eggs than the spring spawning race which resulted in the alevins of spring spawners having lower survival to first feeding. Given the greater survival probability of larger eggs the Rannoch planktivorous population would be expected to experience lower mortality rates in early life while the benthivorous and piscivorous would be expected to experience higher mortality rates. This prediction fits the observed values for planktivorous and benthivorous forms (Figs 5.10 a and b) with unovulated eggs experiencing mortality rates of 99.13% and 99.68% to the end of the first year of life (age 0+) . The piscivorous morph however, despite having small eggs has, according to my estimations, the lowest total fecundity and the lowest unovulated egg to age 0+ mortality rates (99.12%) of all three morphs. This could be explained by the fact that benthivorous fish spawn at greater depth thus their eggs are less susceptible to predation by brown trout which have a strong tendency to feed in the littoral zone and have been found, as well as planktivorous charr caught in the littoral zone during spawning time, to contain charr eggs. It is possible that the piscivorous morph can, by utilising the abyssal zone, where egg predation is lower, survive with a relatively low level of reproductive investment.

Information on the reproductive investment by age class is an important tool in the management of fish populations. The data provided in Fig. 5.10 give an approximation of the relative importance of each age class to the overall reproductive output of each population given our lack of knowledge about the abundances of certain age classes. This information reveals that all three morphs differ greatly in this respect. Any proposed exploitation of these, as with all sympatric populations should therefore recognise the uniqueness of each spawning population (morph) with respect to its abundance, ecology and life history (Behnke, 1972; Ricker, 1972; Ferguson and Taggart, 1991).

CHAPTER 6 - HABITAT UTILISATION, TROPHIC SPECIALISATION AND PATTERNS OF PARASITIC INFECTION IN ARCTIC CHARR AND BROWN TROUT IN LOCHS RANNOCH, ERICHT AND TAY.

6.1 Introduction

Throughout much of their northern European range, Arctic charr are frequently sympatric with brown trout, these two species often being the only numerically significant species in many lakes (Nillson, 1955). In certain circumstances the charr populations may exhibit trophic polymorphism. Thus three or more trophic specialists (two or more charr morphs and brown trout) may exist that differ in their competitive ability with regard to habitat and prey utilisation resulting in partitioning of resources and segregation in habitat. While dietary and habitat differences amongst charr morphs from polymorphic populations are well documented (e.g. Hindar and Jonsson, 1982; Sandlund *et al.*, 1992), dietary and habitat utilisation of sympatric brown trout have not been considered in relation to the sympatric charr in lakes which contain trophic morphs of charr.

In allopatry, brown trout and Arctic charr are reported to have similar dietary and habitat preferences, both feeding on amphipods, gastropods, ephemeropteran nymphs and terrestrial arthropods and both occupying the littoral zone (Nillson, 1963; 1965). In sympatry, trout exhibit similar habitat utilisation and prey choice as they do in allopatry. Arctic charr, however, utilise a more pelagic habitat when found in sympatry with brown trout where they consume predominantly zooplankton (Hegge *et al.*, 1989; Langeland *et al.*, 1993; Jensen *et al.*, 1997).

Additionally, both species may undergo ontogenetic dietary shifts, such as the adoption of piscivory or cannibalism (L'Abée-Lund *et al.*, 1992; Amundsen, 1994).

Determination of dietary specialisations using conventional stomach analysis does have a major drawback in that it only provides information on the prey consumed within the preceeding days or hours (Curtis *et al.*, 1995). However, the presence of certain parasites within a potential host can provide long term information on the hosts past prey selection (Bérubé and Curtis, 1986; Knudsen, 1995; Curtis *et al.*, 1995; Dorucu *et al.*, 1995; Knudsen *et al.*, 1996). Arctic charr and brown trout are each potential intermediate hosts for plerocercoids of pseudophyllidean parasites of the genus *Diphyllobothrium* (*D. dendriticum and D. ditremum*). Eggs of the parasite are released in birds faeces from which coracidia hatch out, these are ingested by a copepod and develop into procercoids therein. The copepod is then ingested by a fish in which the parasite develops into the plerocercoid stage. The life cycle is completed when the infected fish is ingested by a piscivorous bird (Schmidt and Roberts, 1989). Plerocercoids of the parasites encyst on the internal organs of the fish and are highly visible: typically *D. ditremum* is restricted to the digestive tract whereas *D. dendriticum* also occurs throughout the body cavity (Henricson, 1977). Curtis *et al.*, (1995) and Knudsen *et al.*, (1996) thus found that charr infected with *Diphyllobothrium* also tended to contain copepods in their stomachs. A further potential mechanism whereby fish can become infected with *Diphyllobothrium* is by the consumption of prey fish which are themselves infected. Such transmission is known as paratenic transmission

(Halvorsen and Wissler, 1973) and can lead to particularly high parasite burdens in piscivorous fish (Curtis, 1984)

Charr and trout are potential hosts for the acanthocephalan worm *Echinorhynchus truttae*. Fish, the definitive host of this parasite, become infected as a result of consuming the intermediate host of this parasite, the amphipod *Gammarus* (Awachie, 1965). The presence of this parasite in the intestine of a fish would therefore indicate that *Gammarus* had at some time been part of the fish's diet. The presence of these two parasites are likely to provide strong indications as to the extent that fish are adopting planktivory, piscivory and benthivory.

Using conventional stomach contents analysis and an analysis of parasitic loading to determine trophic status and catch rate in gill nets set in three habitat zones I compared habitat use and dietary relationships of Arctic charr and brown trout from all three study lochs.

6.2 Materials and methods

Field sampling

The material used in this analysis was collected during several sampling trips carried out as part of a number of ongoing studies. The depth at which sampling gill nets were set were selected depending on the catch requirements of the particular sampling occasion, although generally littoral, sub-littoral and profundal zones were sampled. Multi-panelled benthic gill nets (8 panels, knot to knot mesh size ranging from 8-50mm) were set at depths recorded by a hand held depth sounder and allowed to fish for periods of approximately 24h. On retrieval of nets, fish species and morphs of charr caught were identified and the depth from which they were captured was recorded. Fish were frozen within 6h of retrieval from nets.

In addition to fish sampling, quantitative zooplankton sampling was conducted in L. Rannoch from March to June, 1995. This was done by towing a Clarke-Bumpus plankton sampler at a depth of 1m for approximately 10 seconds. At least three samples were taken on each occasion with a separation of several hundred metres between sampling locations. The contents of the collecting funnel were transferred to a storage bottle to which 95% ethanol was added to preserve the sample. Each storage bottle was labelled with the volume of water filtered, as read by the plankton sampler.

Laboratory procedure

After thawing, fish were dissected to allow examination of all internal organs. The number of encysted plerocercoids of *Diphyllobothrium* sp. (*D. dendriticum* and *D. ditremum*) were recorded. All prey items and parasites contained in the stomach, pyloric cecae and intestines were removed and stored in 70% ethanol for later examination and identification. Prey items were identified by examination under a dissecting microscope. Where fish were found in stomachs and were not sufficiently intact to make an identification of species or morph, trout were discriminated from charr by examination of the shaft of the vomer bone. Arctic charr have a short, toothless vomer shaft, whereas trout have a long, toothed vomer shaft (Maitland and Campbell, 1992). Discrimination of piscivorous from planktivorous charr was made on the basis of jaw structure, (chapter 2; Adams *et al.*, in press). Prey items were recorded as present or absent in each individual and expressed as percentage occurrence (Hyslop, 1980). Acanthocephalan worms were identified to species level by examination under a dissecting microscope and by reference to the taxonomic key in Brown *et al.* (1986).

Plankton was counted by transferring the contents of the sample bottle to a cell of a plankton microscope and counting all individuals of all species.

Data analysis

To allow a statistical comparison of parasite burden amongst fish groups, where parasite number increased with fork length, the number of worms were standardised using the equation of Ihssen *et al.* (1981):

$$M_t = M_o (L_m/L_o)^b$$

where

L_o = fork length for individual fish

L_m = mean fork length for all fish

M_t = size corrected worm count

M_o = the uncorrected worm count

b = the pooled regression coefficient of $\log_e M_o$ on $\log_e L_o$

The number of *Diphyllobothrium* plerocercoids increased significantly with fork length (Log_e cyst number = -10.9 + 2.46 $\log_e$ fork length; $F_{1,146}=53.02$, $p<0.001$). Comparisons of *Diphyllobothrium* infections amongst populations were therefore made on size corrected values. No significant relationship was found between fork length and number of *E. truttae* ($F_{1,104}=2.41$; $p=0.123$) so correction for fish size was not necessary.

6.3 Results

Habitat segregation

Catch data showed a clear trend in all three lochs, with brown trout being caught in the shallowest nets and charr being caught at greater depths. Sampling during the spring in L. Tay (Table 6.1) indicated that significantly more trout were caught at 5m and 10m combined than at 25m and 40m combined ($\chi^2=16.3$, d.f.=1 $p<0.0001$). Sampling of L. Rannoch in spring (Tables 6.2 and 6.3) revealed a similar pattern with trout being caught at 1m and 10m only and charr only being caught at 30m and 60m. Catches of piscivorous charr were made at significantly greater depths than planktivorous charr (data from tables 6.2 and 6.3 combined, $\chi^2=8.1$, d.f.=1, $p<0.005$) and these were the only fish caught at 60m.

In contrast to this, during the spawning period planktivorous charr were caught in high numbers in the L. Rannoch littoral zone (Table 6.4). Thus no significant difference between catches at 1m and 10m combined and 20 and 45m combined existed between trout and planktivorous charr ($\chi^2=0.23$, d.f.=1, $p=0.631$) or between trout and planktivorous and piscivorous charr combined ($\chi^2=1.16$, d.f.=1, p=0.282) in L. Rannoch at this time. However, trout were the only species caught at 1m and the only species not caught at 45m. Significantly more piscivorous charr were caught at depth than were trout and planktivorous charr combined (χ^2=21.87, d.f.=1, p<0.0001).

Simultaneous sampling of the pelagic and littoral zone of the east basin during the summer indicated that only planktivorous charr and trout were present in the pelagic zone (surface to 5m depth; Table 6.5), whereas trout, planktivorous charr and piscivorous charr were present in the littoral zone (2m, 10m and 14m nets). Again there was some suggestion of depth segregation, with trout having the shallowest depth range and piscivorous charr having the deepest depth range, although low sample sizes prevented statistical analysis of this. No difference was found in the relative abundance of trout and planktivorous charr in the littoral (2m, 10m and 14m nets) and pelagic zones (χ^2 = 0.475, d.f.=1, p=0.491).

Catches of fish outwith the spawning season in L. Ericht (Table 6.6) were not sufficiently large to allow statistical analysis of depth segregation although they show a similar trend to L. Rannoch trout and charr. During the spawning season (Table 6.7 and 6.8) planktivorous charr were caught in high numbers in the littoral zone and were caught in significantly proportionately higher numbers at 15m than at the two greater depths (data from Tables 6.7 and 6.8 combined, χ^2 = 23.96, d.f.=1, p<0.001).

Table 6.1 Number of fish caught at each sampling depth in L.Tay: 30/3/97.

	5m	10m	25m	40m
trout	4	7		1
charr			4	4

Table 6.2 Number of fish caught at each sampling depth in L. Rannoch: 10/4/96.

	10m	30m	60m
trout	15		
planktivorous charr		5	
piscivorous charr		10	6

Table 6.3 Number of fish caught at each sampling depth in L. Rannoch 9/5/96.

	1m	10m	30m	60m
trout	2	6		
planktivorous charr			5	
piscivorous charr				5

Table 6.4 Number of fish caught at each sampling depth in L. Rannoch 9/10/96.

	1m	10m	20m	45m
trout	3	5	3	
planktivorous charr		53	26	2
piscivorous charr			1	13

Table 6.5 Number of fish caught at each sampling depth in L. Rannoch 5/6/97.

	2m	10m	14m	pelagic
trout	2	3		14
planktivorous charr	2	4	1	31
piscivorous charr		4	7	

Table 6.6 Number of fish caught at each sampling depth in L. Ericht 20/5/96.

	15m	25m	40m
trout	22		
planktivorous charr		2	
piscivorous charr			2

Table 6.7 Number of fish caught at each sampling depth in L. Ericht 17/10/96.

	15m	25m	40m
trout	3		
planktivorous charr	98	1	
piscivorous charr	1		3

Table 6.8 Number of fish caught at each sampling depth in L. Ericht 22/10/96.

	20m	30m	40m
trout			
planktivorous charr	80	15	10
piscivorous charr	2		4

Comparative catches in east and west basins of L. Rannoch

Comparison of catches between east and west basins during the summer (Table 6.9) showed that benthivorous fish were significantly more abundant in the west than east basin ($\chi^2 = 47.43$, d.f.=1, $p<0.0001$), with only one benthivorous fish being caught in the east basin and piscivorous fish entirely restricted to the east basin. A similar segregation was found in the spring with benthivorous and piscivorous charr entirely confined to the west and east basins respectively and during the spawning period ($\chi^2 = 511.7$, d.f.=1, $p<0.001$). Pike and perch were almost entirely confined to the west basin.

Dietary segregation

A comparison of the three L. Rannoch charr morphs (presented in chapter 2) with sympatric brown trout during summer and autumn is presented in Fig. 6.1. A large number (44%) of trout were found to contain trichoptera larvae, this being their most commonly consumed prey item. A number of trout were also found to contain cladocera, although these were exclusive to trout caught in the early summer. Terrestrial insects were exclusively found in trout (10% of individuals) as were ephemeroptera larvae (present in 5% of individuals).

As with L. Rannoch trout, L. Ericht trout consumed large numbers of trichoptera larvae (present in 38% of individuals), although these was also present in 25% of piscivorous charr (Fig. 6.2). The main prey item of trout was surface insects, present in 45% of individuals. This prey group was not represented in either charr groups as was the case with coleoptera, ephemeroptera larvae and gastropoda. The

Table 6.9 Number of fish caught in west and east basins of L. Rannoch. Dates refer to time of sampling.

	9/5/96		5/6/97		Oct-Nov (1994-96)	
	west	east	west	east	west	east
piscivorous	0	10	0	11	0	310
benthivorous	10	0	41	1	211	3
planktivorous	3	5	4	7	841	47
trout	1	8	3	5	27	288
perch	2	0	>100	0	>300	21
pike	0	0	0	0	12	2

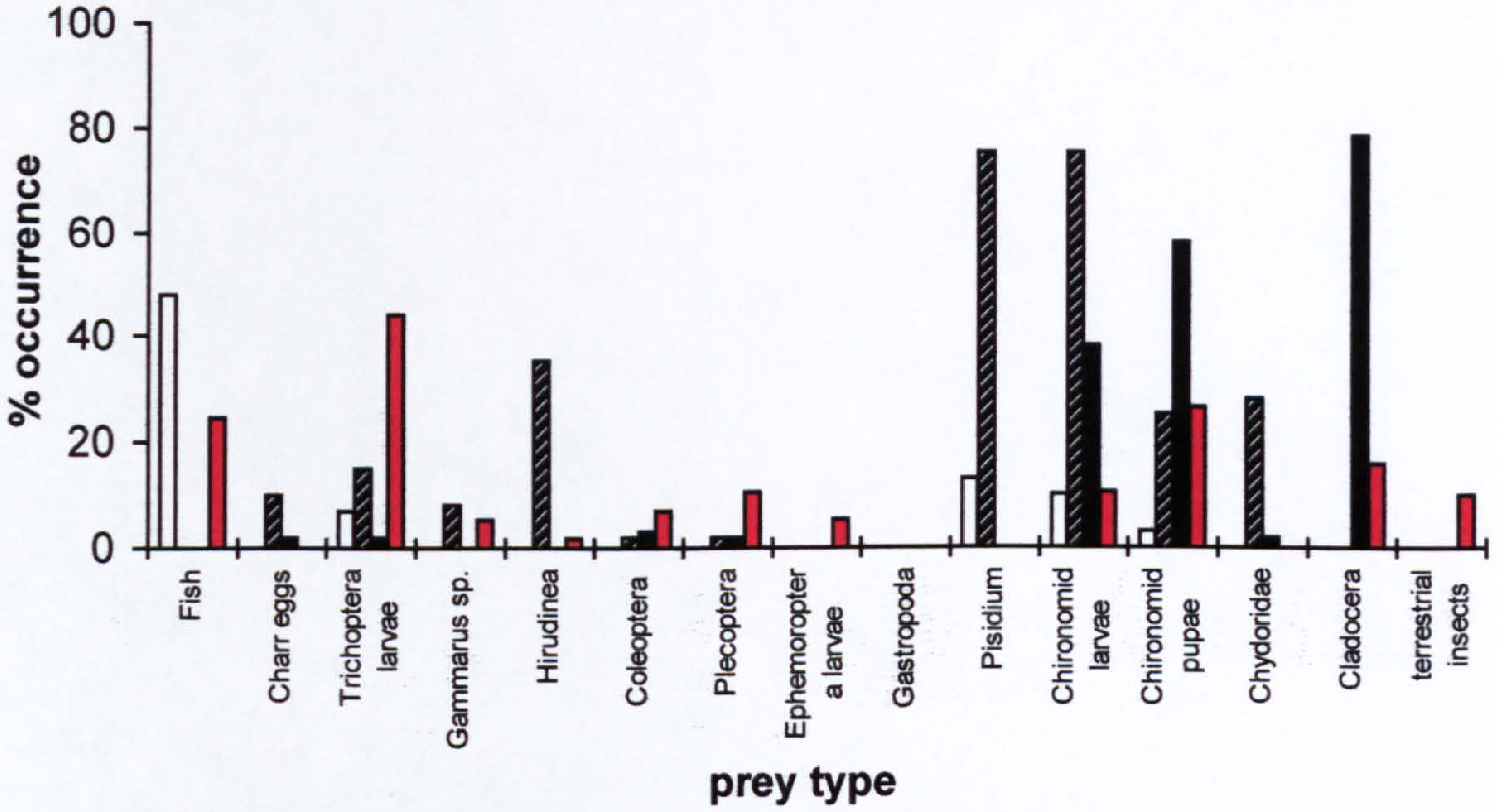

Figure 6.1 Percentage occurrence of prey items identified in charr and trout from L. Rannoch during summer and autumn. Planktivorous charr = ■, piscivorous charr = □, benthivorous charr = stippled bars, brown trout = 🟥.

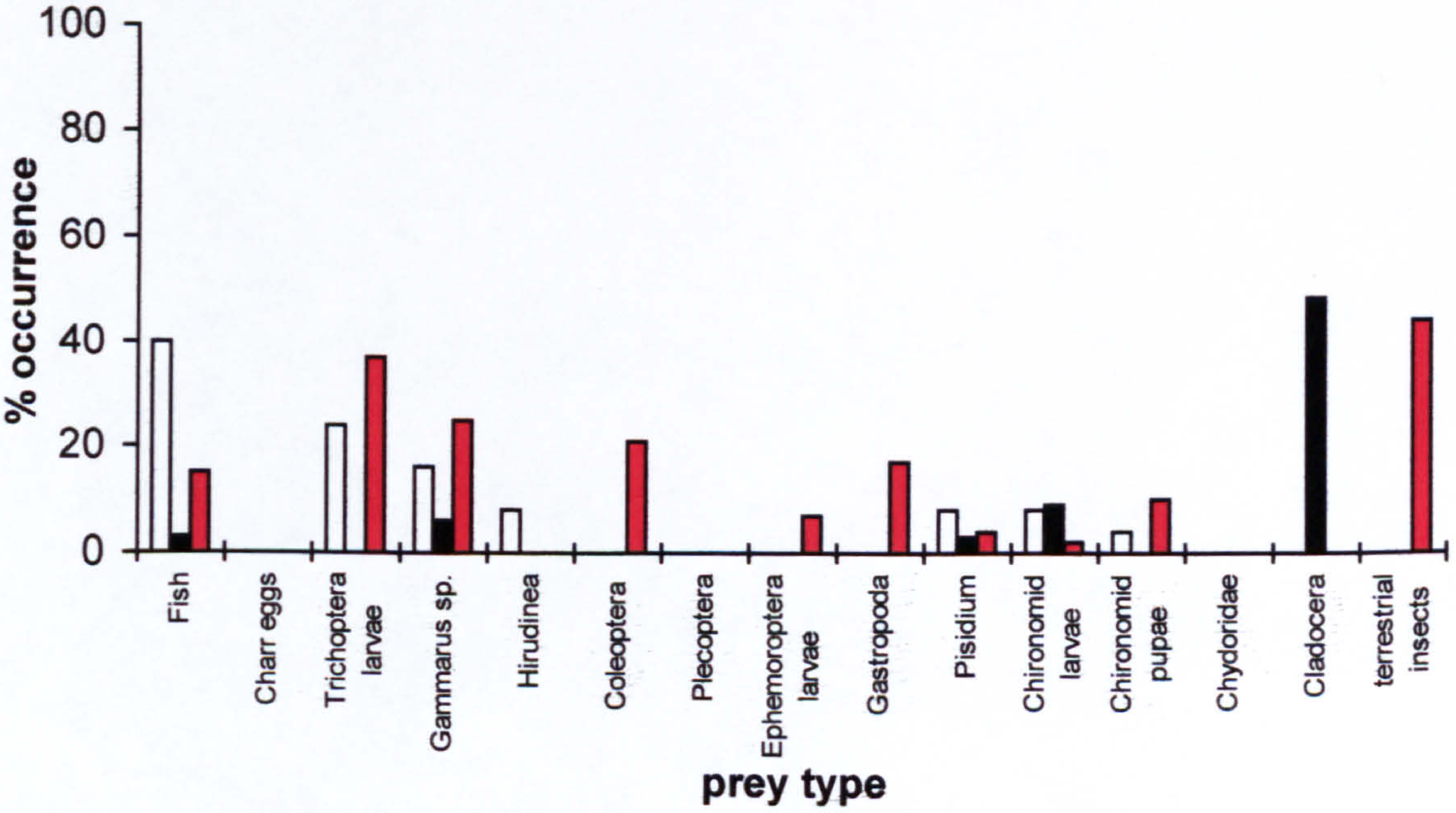

Figure 6.2 Percentage occurrence of prey items in charr and trout from L. Ericht. Spring, summer and autumn samples combined. Planktivorous charr = ■, piscivorous charr = □, brown trout = 🟥.

third most frequently consumed prey item of trout was *Gammarus* sp., present in 26% of trout although also present in 16% and 8% of piscivorous and planktivorous charr respectively. Planktivorous charr were the only group to consume zooplankton, this being their main prey item (present in 48% of individuals). Piscivorous charr mainly consumed fish (present in 40% of individuals) although piscivory was also observed in trout (present in 15% of individuals) and in a single planktivorous charr which contained a threespined stickleback.

Seasonal variation

Seasonal shifts in diet were evident in L. Tay charr (Fig. 6.3) which similarly to L. Ericht and Rannoch planktivorous charr consumed zooplankton almost exclusively in the summer and autumn, but when trout and charr were sampled in March, each was foraging on similar prey items, such as trichoptera larvae and other benthic organisms despite the two species being segregated in habitat (Table 6.1). A seasonal comparison of diet in trout was not possible as very few trout were caught outwith the spring.

Loch Rannoch planktivorous charr, as with L. Tay charr showed a clear seasonal dietary switch from benthic prey items in April (Fig. 6.4) to planktivorous prey in June, this switch corresponded to a increase in temperature from 4.5°C to 10.2° and zooplankton from 0.73 to 8.09 plankters per litre (Fig. 6.5). Principal prey items were chironomid larvae and pupae, (present in 85% and 75% of individuals respectively) followed by *Pisidium* sp. and trichoptera larvae, present in 50% and

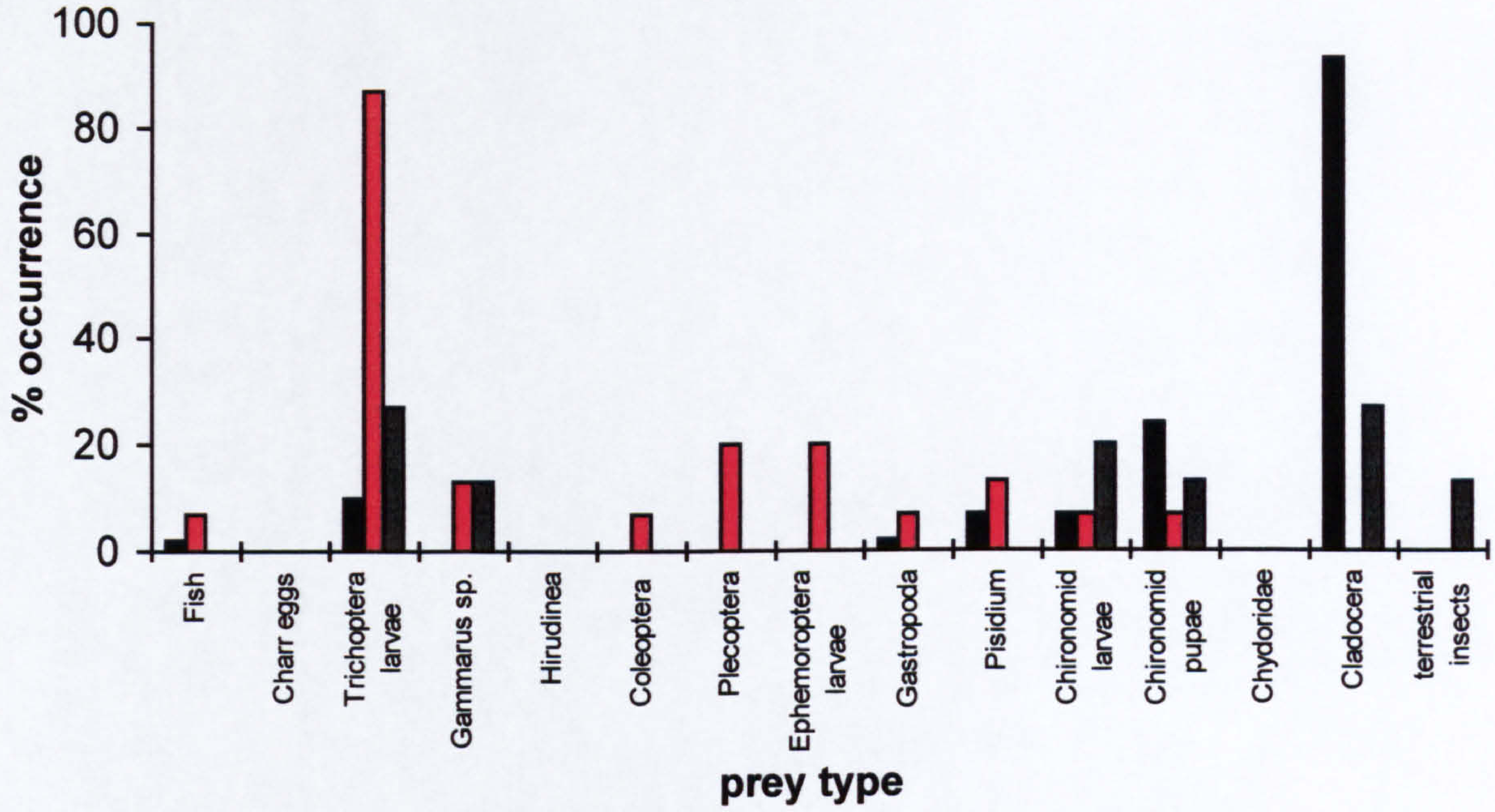

Figure 6.3 Percentage occurrence of prey types identified in charr in L. Tay in July and October (■) and March (▒) and brown trout in March (🟥).

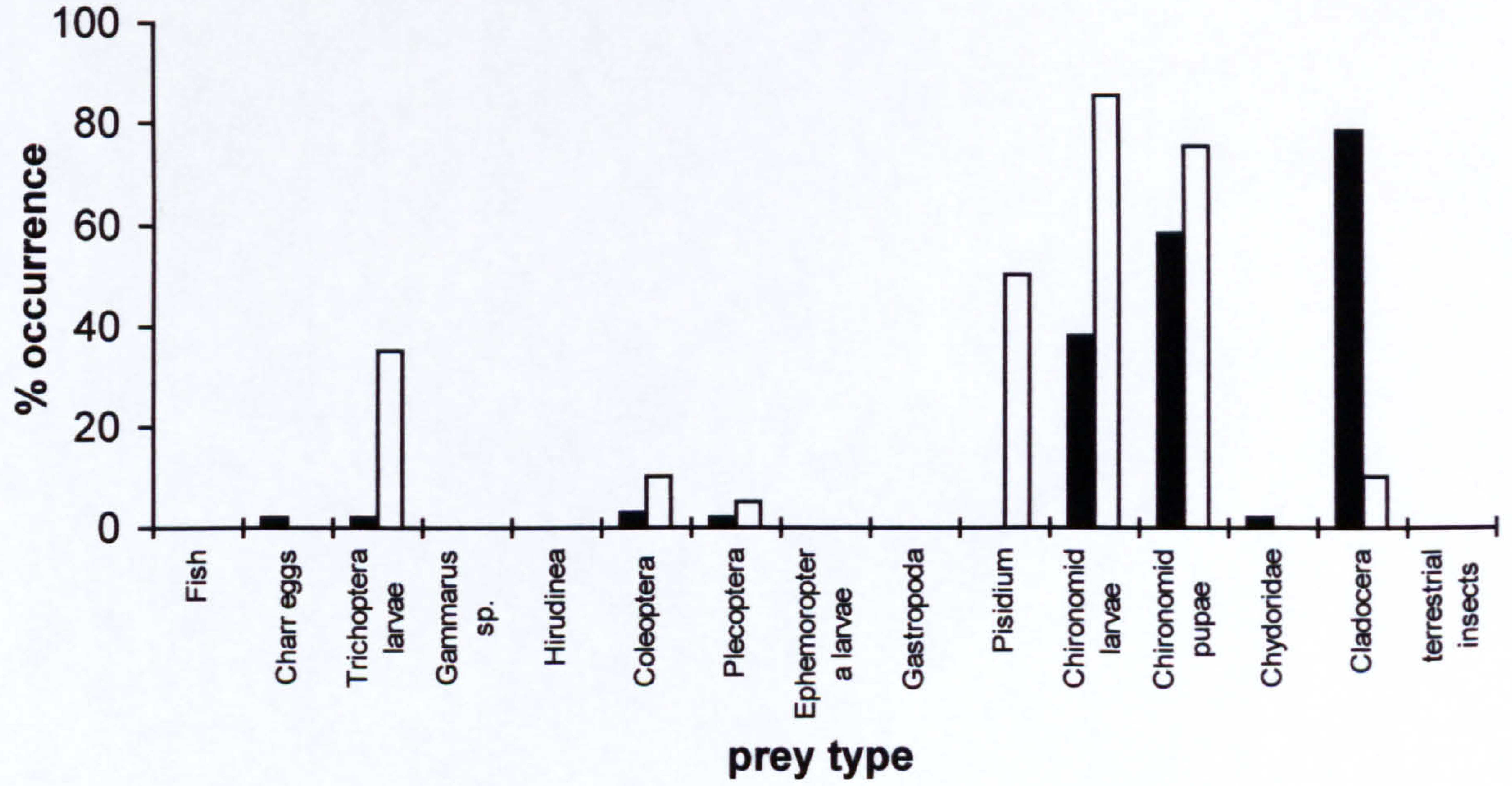

Figure 6.4 Percentage occurrence of prey items identified in L. Rannoch planktivorous charr during a period of high (■) and low (□) zooplankton abundance (June and April respectively).

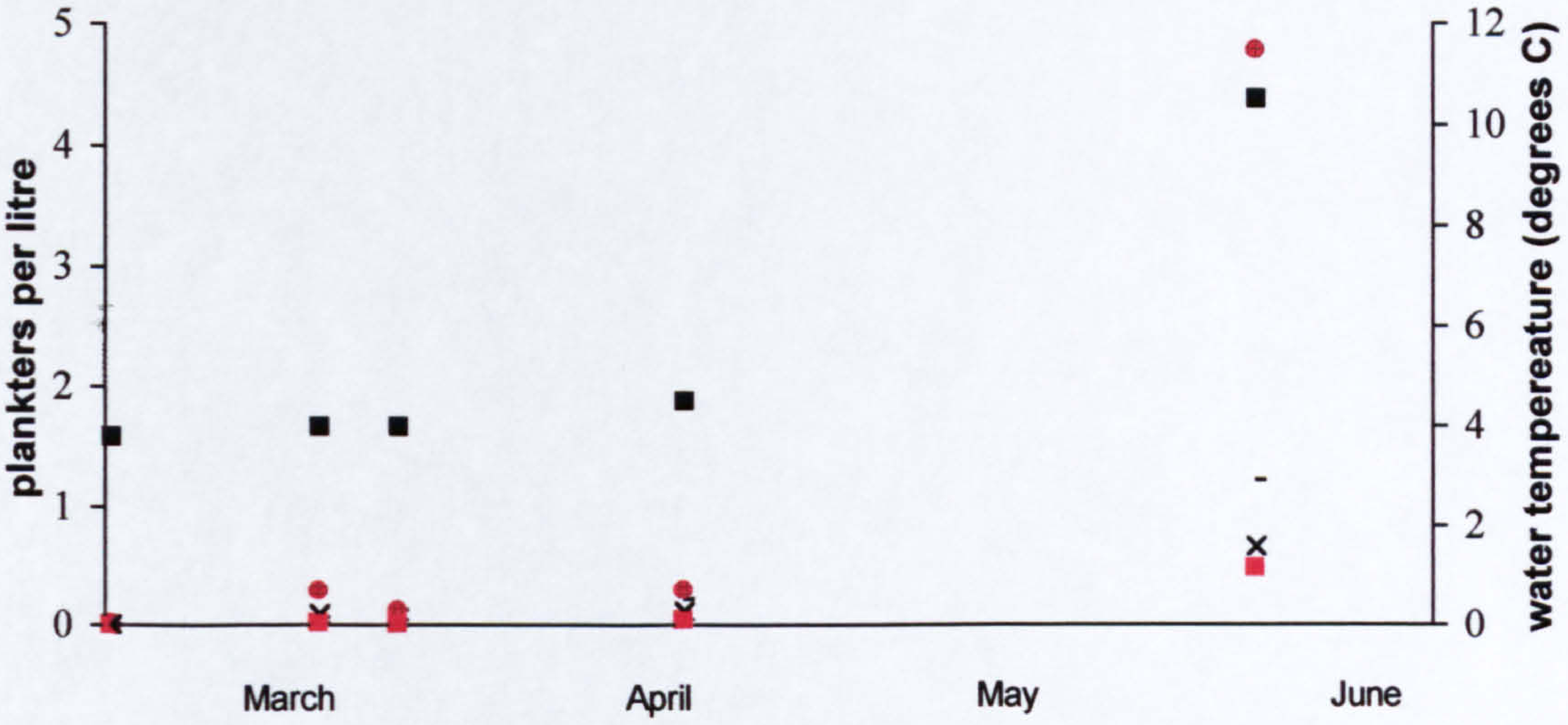

Figure 6.5 Change in water temperature (■) and zooplankton density in L. Rannoch from March - June 1995. • = *Bosmina*, ■ = *Daphnia*, x = *Cyclops*, - = *Diaptomus*.

35% of individuals respectively. Only 10% of individuals contained cladocera. Analysis of stomach contents weight in L. Rannoch planktivorous charr in April and June indicated that stomach contents weight was significantly related to fork length (stomach weight = -0.584+0.00505 fork length, $F_{1,14}$=16.74, p<0.001 R^2=; stomach weight = -4.39+0.0288 fork length, $F_{1,8}$=20.85, p<0.001, R^2=68.8% respectively). No relationship was found between stomach weight and fork length during October (stomach weight =-0.218+0.00333fork length, $F_{1,26}$=2.54, p=0.123, R^2=5.4%). Covariance analysis indicated that planktivorous charr had significantly fuller stomachs in June than in either April or October ($F_{1,22}$=23.53, p<0.001; $F_{1,34}$=24.78, p<0.001). No differences were found between stomach weights in April and October in regression gradient or elevation ($F_{1,40}$=0.537, p=0.536; $F_{1,41}$=0.31, p<0.578).

Piscivory

The extent of piscivory varied in piscivorous charr and trout as did the length at which it was first observed (Fig. 6.6). Thus 71% of L. Ericht piscivorous charr contained fish in length classes above 160mm, the class in which piscivory was first observed. The corresponding values were 52% and 180mm for L. Rannoch piscivorous charr, 24% and 200mm for L Ericht trout and 26% and 220mm for L. Rannoch trout. The proportions of individuals above the threshold at which piscivory first occurred, actually containing fish was not significantly different between L. Rannoch and L. Ericht trout (χ^2 = 0.04, d.f.=1, p=0.841) or between L. Rannoch and L. Ericht piscivorous charr (χ^2 = 1.89, d.f.=1, p=0.841). Comparison of the two trout populations combined, with the two piscivorous

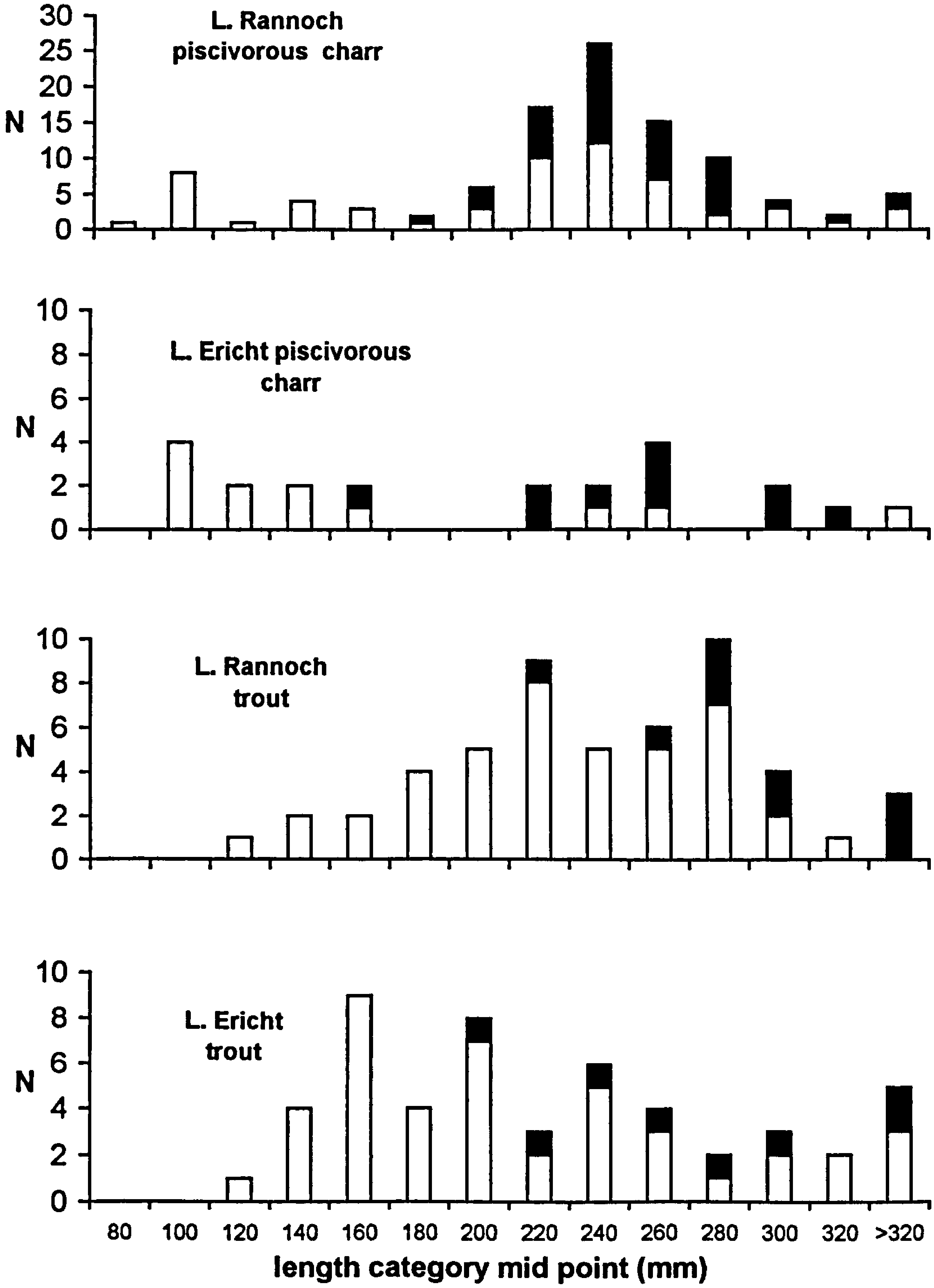

Figure 6.6 Length frequency distribution of the four piscivorous fish groups. Individuals containing fish = ■, individuals not containing fish = □.

charr populations combined, indicated that significantly more piscivorous charr contained fish than trout ($\chi^2 = 14.46$, d.f.=1, $p<0.001$).

Of the prey fish that could be positively identified, piscivorous charr were the main prey of piscivorous charr in loch Rannoch (Table 6.10) and the only prey type identified in L. Ericht piscivorous charr. Loch Rannoch trout contained mainly charr, two of which could be positively identified as piscivorous charr. Threespined sticklebacks were the most common positively identified prey fish in L. Ericht brown trout although salmonids (including charr) also featured in their diet.

Patterns of parasitic infections

Loch Rannoch: Comparison of the proportion of individuals infected with *Diphyllobothrium* sp (Fig. 6.7) indicated that 76% of planktivorous charr harboured plerocercoids, this value being significantly higher than for trout and piscivorous charr ($\chi^2 = 26.72$, d.f. =2, $p<0.001$), which themselves did not differ in the proportion of fish infected (29% and 30% of individuals respectively; $\chi^2 = 0.08$, d.f.=1, p=0.781). Only 5% of benthivorous charr harboured plerocercoids, this value being significantly less than trout and piscivorous charr ($\chi^2 = 16.74$, d.f.=2, $p<0.001$). *E. truttae* was most frequently recorded in trout (63%), significantly more of which were infected than planktivorous and piscivorous charr ($\chi^2 = 46.3$, d.f.=2, $p<0.001$). Only 8% of planktivorous and 5% of piscivorous charr harboured this parasite, these values not being significantly

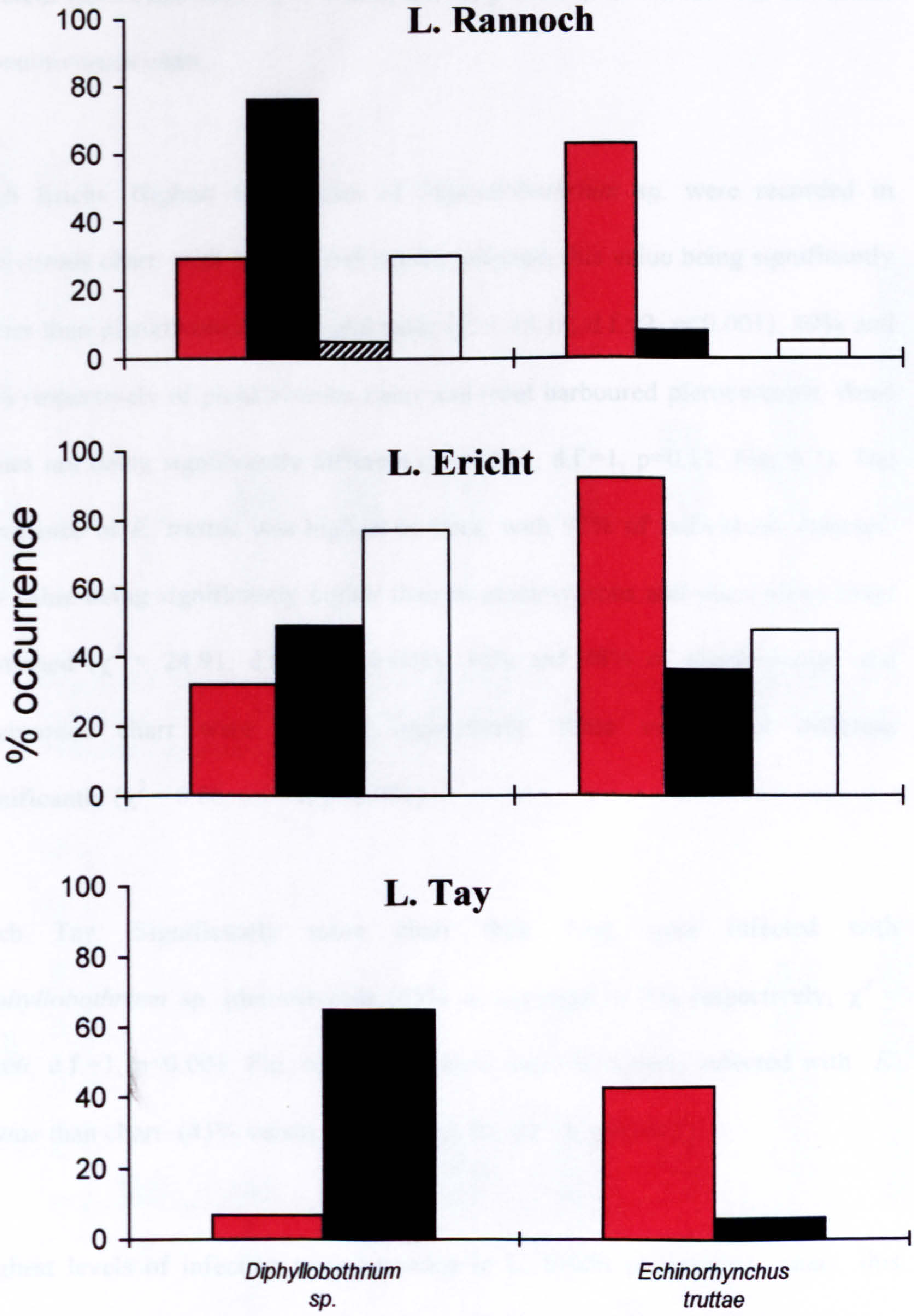

Figure 6.7 Frequency occurrence of *Diphyllobothrium* and *E. truttae* in the fish populations under investigation. Brown trout = 🟥, planktivorous charr = ■, piscivorous charr = □, benthivorous charr = stippled bars.

different from each other ($\chi^2 = 0.368$, d.f.=1, p=0.544). *E. truttae* was not found in benthivorous charr.

Loch Ericht: Highest frequencies of *Diphyllobothrium* sp. were recorded in piscivorous charr, with 77% of individuals infected, this value being significantly higher than planktivorous charr and trout ($\chi^2 = 10.18$, d.f.=2, $p<0.001$). 49% and 32% respectively of planktivorous charr and trout harboured plerocercoids, these values not being significantly different ($\chi^2 = 2.61$, d.f.=1, p=0.11; Fig. 6.7). The prevalence of *E. truttae* was highest in trout, with 92% of individuals infected, this value being significantly higher than in planktivorous and piscivorous charr combined ($\chi^2 = 24.91$, d.f.=1, $p<0.001$), 36% and 48% of planktivorous and piscivorous charr were infected respectively, these values not differing significantly ($\chi^2 = 0.86$, d.f.=1, $p<0.001$).

Loch Tay: Significantly more charr than trout were infected with *Diphyllobothrium* sp. plerocercoids (65% as opposed to 7% respectively; $\chi^2 =$ 13.06, d.f.=1, $p<0.001$; Fig. 6.7). Trout were more frequently infected with *E. truttae* than charr (43% versus 6%, $\chi^2 = 12.59$, d.f.=1, $p<0.001$).

Highest levels of infection were recorded in L. Ericht piscivorous charr, this group having significantly higher numbers of cysts than all other groups except L. Rannoch planktivorous charr (Tukey HSD test, $F_{7,331}=8.37$; $p<0.05$), which had significantly higher numbers of cysts than all trout populations which were not significantly different from each other (Fig. 6.8).

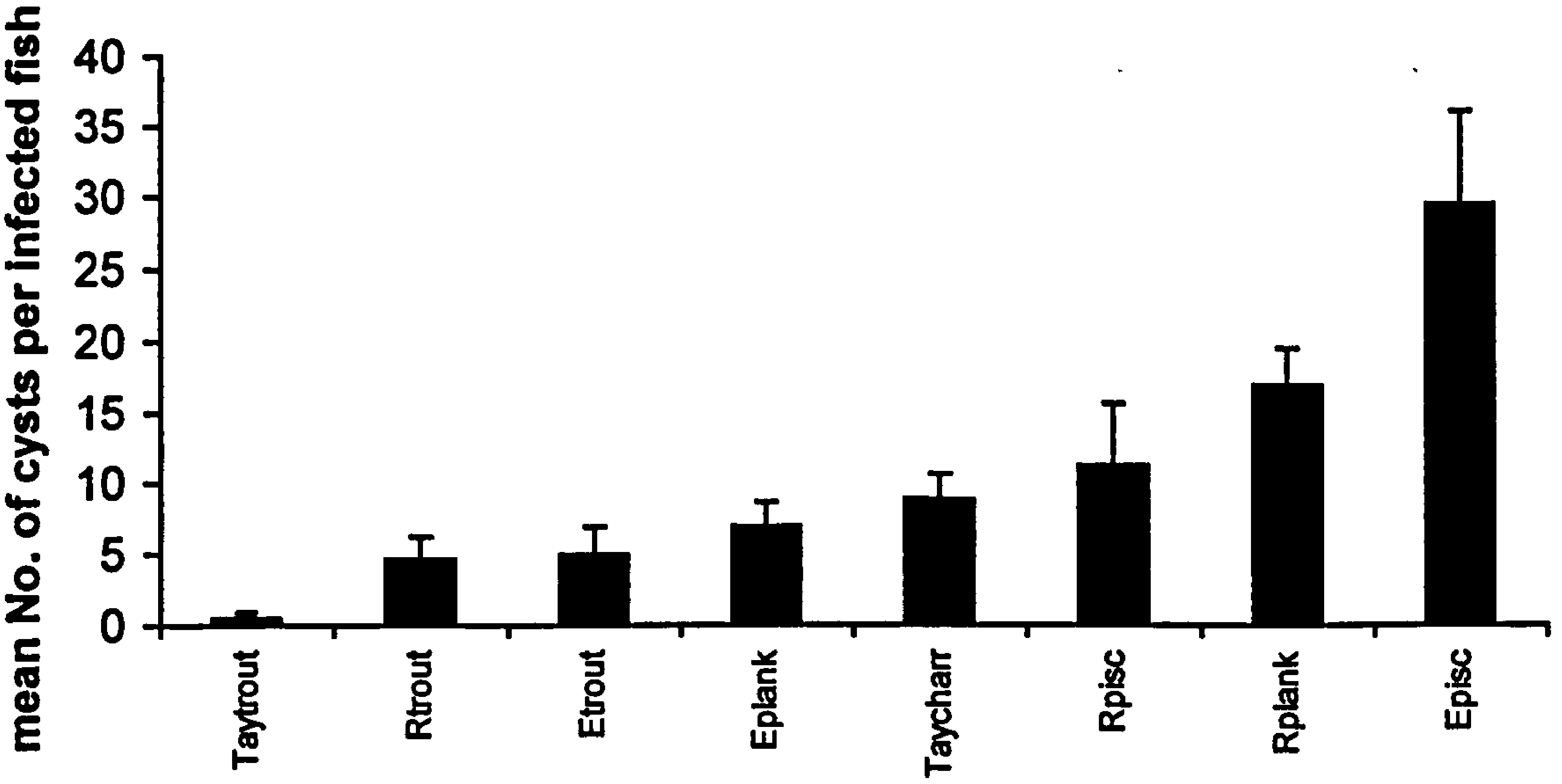

Figure 6.8 Mean number of *Diphyllobothrium* sp. cysts per infected fish in each fish group. Episc, Rplank> Rpisc, Tay charr, Eplank> Etrout, Rtrout, Taytrout. > indicates significance at 0.05 level.

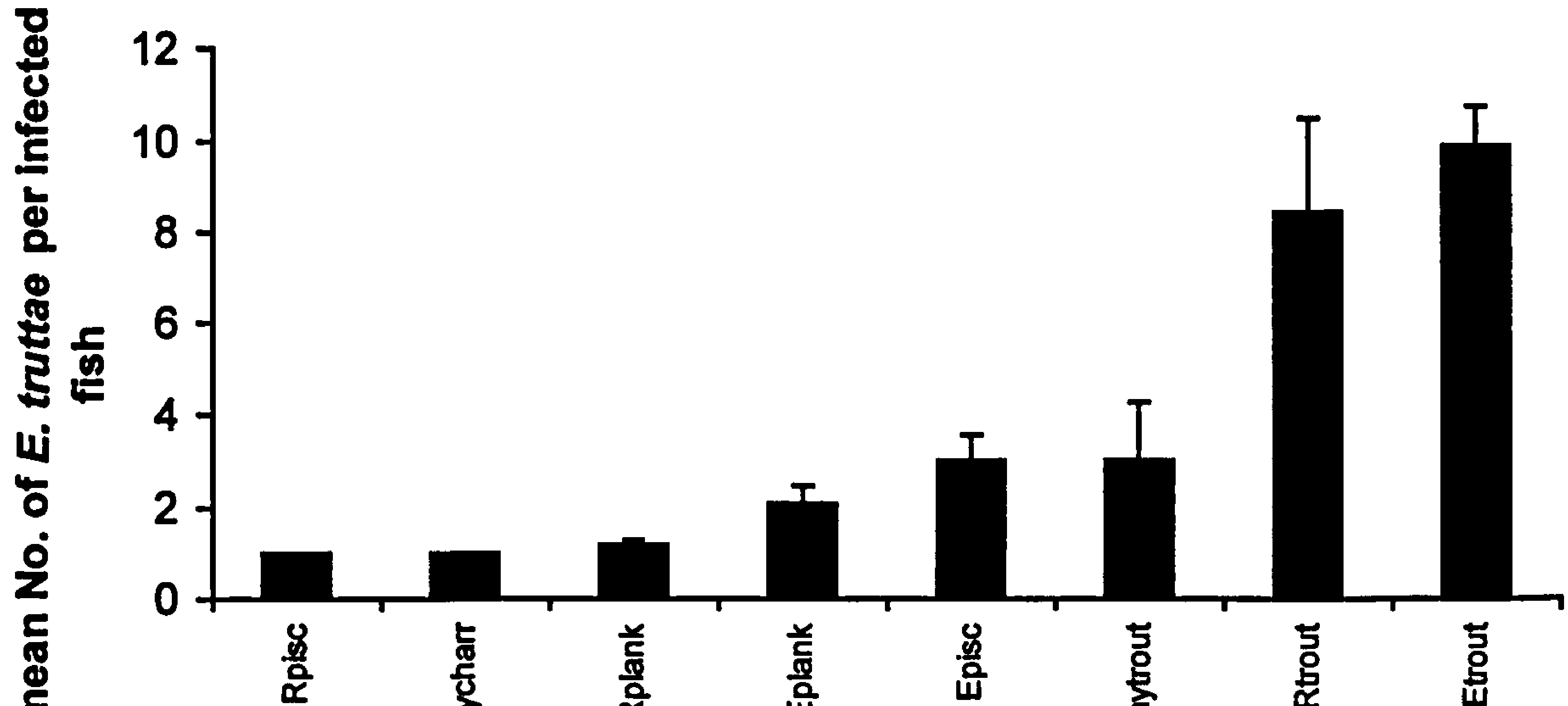

Figure 6.9 Mean number of *E. truttae* per infected fish in each fish group. Etrout> Episc, Eplank, Rplank, Tay charr, Rpisc; Rtrout>Eplank, Rplank, Tay charr, Rpisc > indicates significance at 0.05 level.

Table 6.10 Numbers of various prey fish types in stomachs of piscivorous charr and trout from L. Rannoch and Ericht.

	trout		piscivorous charr	
	L. Rannoch	L. Ericht	L. Rannoch	L. Ericht
indeterminate salmonid	1	3	25	8
piscivorous charr	2		10	3
planktivorous charr				
indeterminate charr	6	1	4	
trout		1	1	
3-spined stickleback	1	4		

No significant differences in the mean number of *E. truttae* per infected fish were found amongst the three trout populations which harboured the most parasites (Fig. 6.9). Infected L. Ericht trout harboured significantly more *E. truttae* than L. Ericht and Rannoch planktivorous charr and L. Ericht piscivorous charr, whereas L. Rannoch trout harboured significantly more *E. truttae* than L. Ericht and Rannoch planktivorous charr (Tukey HSD test, $F_{7,104}=8.35$; $p<0.05$).

The length at which individuals of each population acquired *Diphyllobothrium* plerocercoids varied. In L. Rannoch there was a progressive decrease in the fork length at which plerocercoids were first observed from 220mm in trout, 200mm in piscivorous charr and 160mm in planktivorous charr (Fig. 6.10). In L. Ericht trout, plerocercoids were recorded in two individuals in length class 160mm although as with L. Rannoch trout, most fish of less than 220mm were uninfected (Fig. 6.11). L. Ericht piscivorous charr were infected as small as 140mm and Planktivorous charr were recorded as being infected at length class 160mm as with L. Rannoch planktivores. Infected L. Tay charr acquired plerocercoids at length class 100mm, the smallest infected fish of all populations examined (Fig. 6.12).

6.4 Discussion

Brown trout and Arctic charr were segregated in a similar manner in all three lochs studied, with brown trout being the predominant species in the littoral zone and charr ocupying deeper and more offshore areas. This finding is in agreement

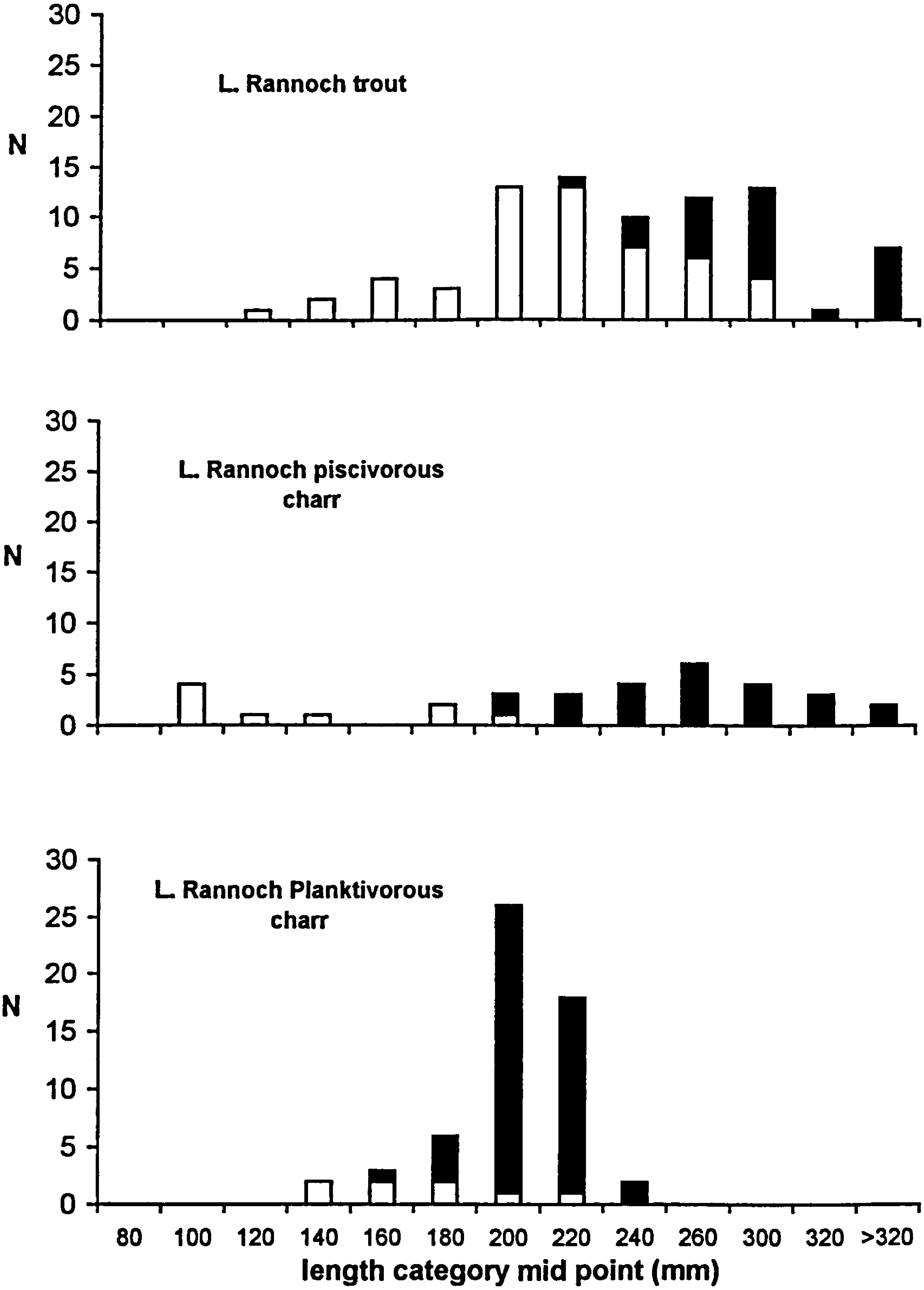

Figure 6.10 Length frequency distribution of L. Rannoch fish populations. Individuals infected with *Diphyllobothrium* = ■, uninfected individuals = □.

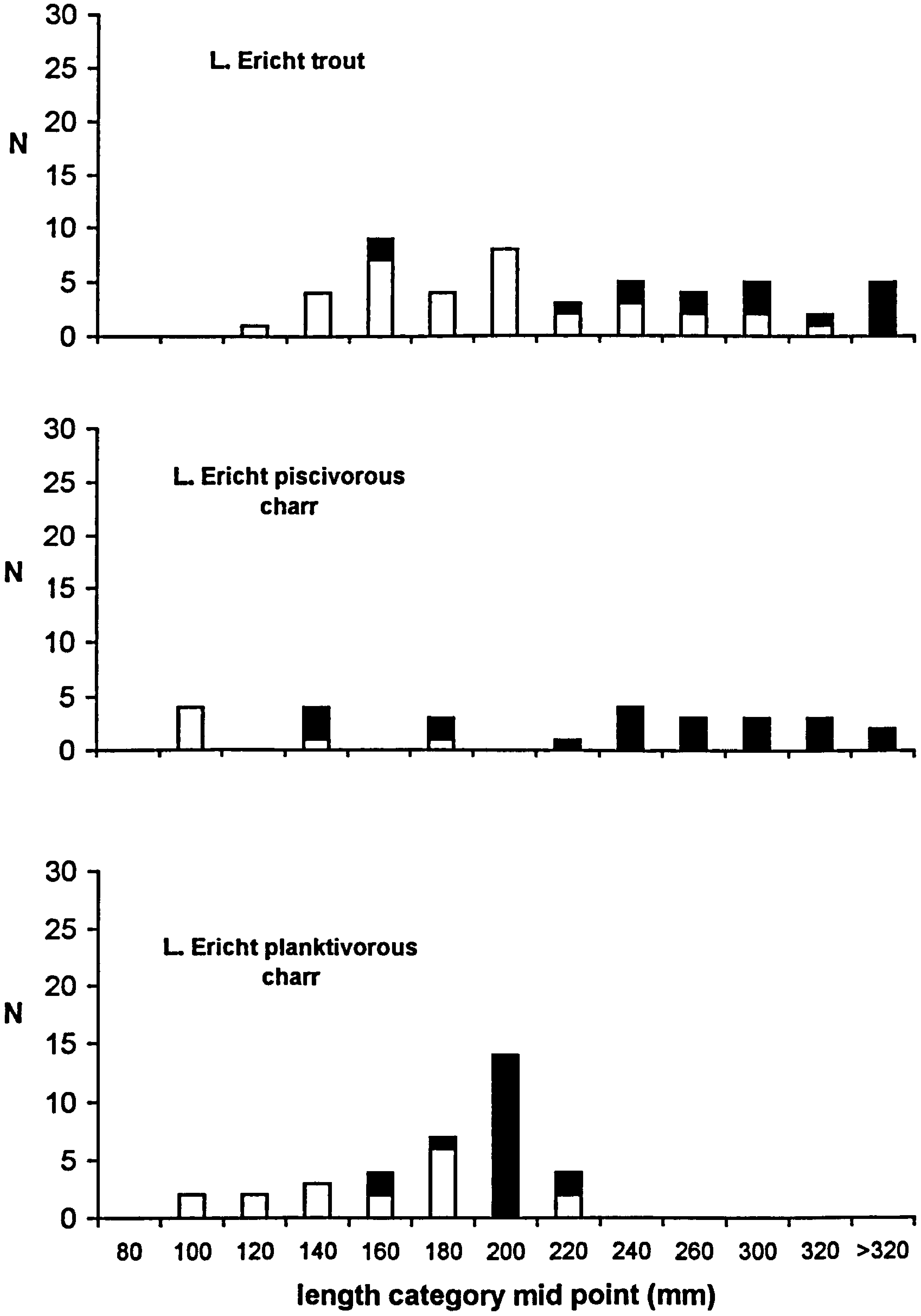

Figure 6.11 Length frequency distribution of L. Ericht fish populations. Individuals infected with *Diphyllobothrium* = ■, uninfected individuals = □.

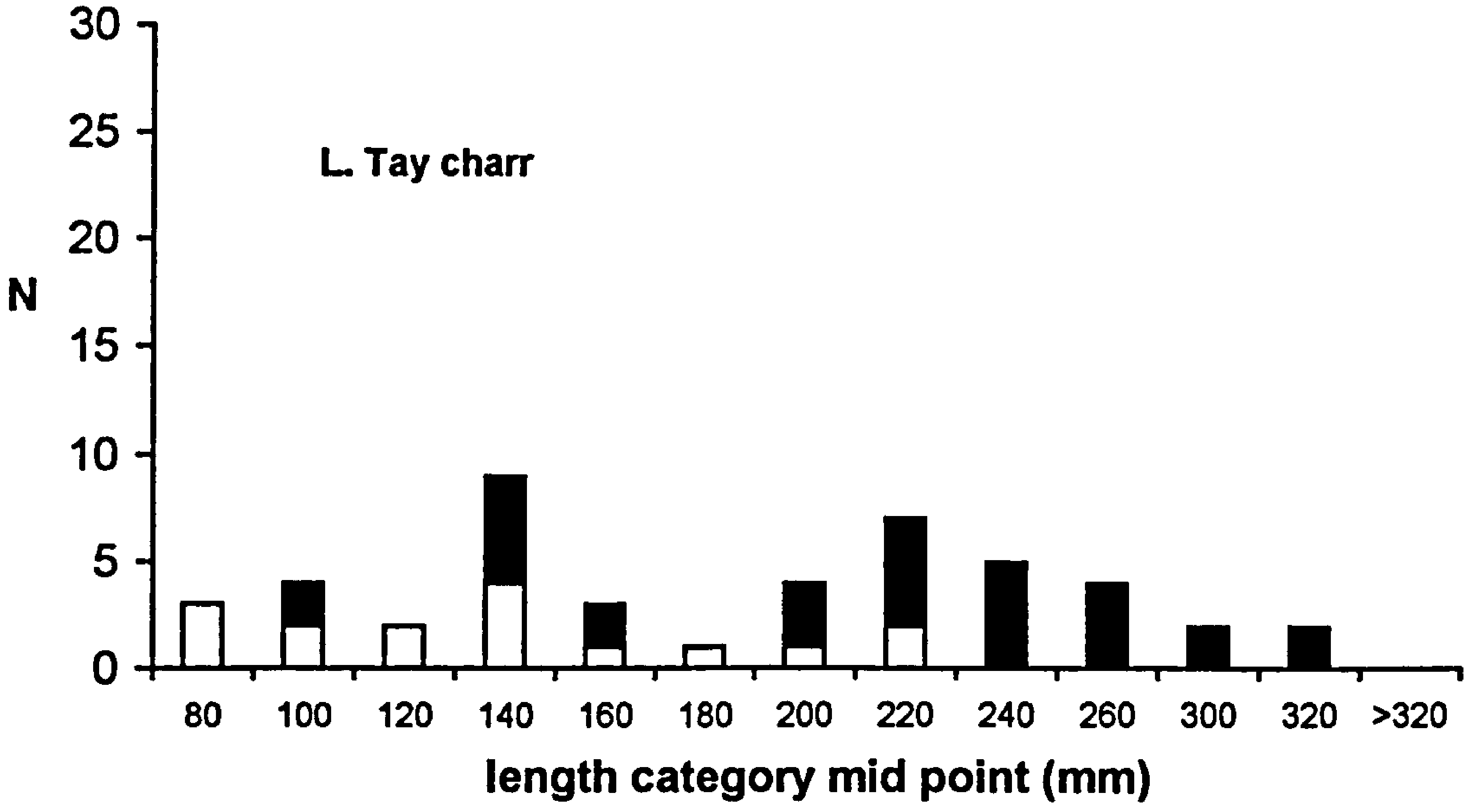

Figure 6.12 Length frequency distribution of L. Tay charr.
Individuals infected with *Diphyllobothrium* = ■, uninfected individuals = □

with those of Langeland *et al.* (1991) who found that in Norwegian lakes, trout exclusively occupied the littoral zone in summer whereas charr occupied pelagic zones and epibenthic zones at greater depths than trout. The finding, at least in L. Rannoch that trout as well as pelagic charr occupy near surface waters in the pelagic zone during summer is in agreement with the findings of Langeland *et al.* (1991) and Hegge *et al.* (1989). In the east basin of L. Rannoch, where two morphs of charr occur, piscivorous charr were caught at significantly greater depths than benthically caught planktivorous charr. In this respect piscivorous and planktivorous charr are analogous to dwarf and normal charr described elsewhere (Jonsson and Hindar, 1982) in that dwarf charr are found to occurr epibenthically at greater depths than normal charr. The complete absence of piscivorous charr from pelagic net catches indicates that, unlike planktivorous charr which can utilise the water column as well as deep abyssal regions, piscivorous charr are restricted to epibenthic abyssal and sub littoral zones. This contention is supported by the observation that when raised in gill nets from depth, piscivorous charr invariably had hugely distended swim bladders as a result of being unable to equilibrate the volume of air in their swim bladders to the lowered water pressure. This was not observed in planktivorous charr raised from the same depth (see chapter 3).

Habitat segregation data from L. Ericht, although less comprehensive than from L. Rannoch, appeared to indicate the same pattern with trout in the littoral zone, benthically occurring planktivorous charr sublittorally and piscivorous charr in deeper water. As with L. Rannoch piscivorous charr, L. Ericht piscivorous charr were unable to adapt to a rapid change in water pressure suggesting that they too are obligate deep water fish (see chapter 3).

In both L. Rannoch and Ericht, planktivorous charr undertook an extensive migration to the littoral zone to spawn in October. Evidence that this habitat shift was for reproductive rather than dietary reasons is provided by the fact that the stomachs of fish caught in the littoral zone contained zooplankton rather than littoral organisms. During this period piscivorous fish were again caught at greater depths indicating that there is some spatial basis to reproductive isolation. The segregation of L. Rannoch benthivorous and piscivorous charr in the west and east basins respectively was not only observed during the spawning period thus maintaining reproductive isolation between the two morphs (chapter 2) but was also observed at other times of the year. This provides strong evidence that it is the existence of these two basins or rather the shallow region between them, that has isolated these two populations given that piscivorous charr appear to be physiologically ill adapted to inhabiting shallow water and that other species i.e. trout and planktivorous charr occupy these shallower regions. Different biotic conditions in the two basins are likely to have selected for the different feeding specialisations observed. For example the west basin contains the only extensive area of aquatic vegetation in the loch (Campbell, 1971). These differences are reflected in the fact that pike and in particular perch are highly abundant in the west basin and almost completely absent from the east basin, an observation also made by Campbell (1971). No systematic sampling by depth was undertaken in the west basin although the general observation was that benthivorous fish were caught in the deeper regions and trout and perch in the littoral zone.

Differences in habitat use were reflected in dietary differences. Thus trout in all three lochs predominantly consumed littoral invertebrates, whereas planktivorous charr in L. Rannoch and Tay consumed zooplankton when abundant in the summer. During the spring when zoopalnkton was less abundant, charr in these two lochs adopted a diet more similar to that of sympatric brown trout. However, the occurrence at greater depth of planktivorous charr at this time indicates that some habitat segregation still exists and this is reflected in the fact that planktivorous charr were still dependant on *Pisidium* and chironomids both of which are associated with soft sediments which occur at greater depths in these lochs (Smith *et al.*, 1981). Data on stomach contents weight from L. Rannoch indicates that charr were limited in their food intake in spring. This is likely to occur for two reasons, firstly, charr are forced into competition with brown trout which, despite charr being more active at low temperatures than trout (Filipsson and Svärdson, 1976), results in charr having to occupy sublittoral and abyssal regions as brown trout are more agressive (Nilsson, 1963) and defend the littoral zone. Secondly, specialised planktivorous charr morphs are morphologically ill apapted to consume benthic prey. No stomach weight data was recorded for trout, so it is not clear how competition with charr at this time affects them.

Piscivorous charr in L. Rannoch and probably L. Ericht occupied the most marginal habitat of all. However, it is possible, given the ability of Arctic charr to locate prey at low light intensities as is the case with the closely related dolly varden charr *Salvelinus malma* (Schutz and Northcote, 1972) they do have some features which make them able to more effectively exploit this habitat. The L. Rannoch (and probably L. Ericht) piscivorous charr are unique in that typically deepwater charr forms are dwarfs, whereas the piscivorous charr described here appear to be highly specialised piscivores, exhibiting an ontogenetic shift to piscivory at 16-18cm and consuming fish almost exclusively at sizes greater than this. In an extensive study of 13 Norwegian lakes, L'Abée-Lund *et al.* (1992) found that piscivory in monomorphic charr populations never exeeded 5% in any one lake and that only two individuals were found to contain other charr, with most piscivorous charr consuming threespined sticklebacks. Piscivory is a common feature in brown trout populations in large, deep oligotrophic lakes of the Scottish Highlands (Campbell, 1979; Greer, 1995) and was observed in all three trout populations examined. In contrast to the study of L'Abée-Lund *et al.* (1992) brown trout in L. Rannoch and Ericht were less strongly piscivorous at sizes above the threshold for piscivory than piscivorous charr. In their study, where threespined sticklebacks were present these were the preferred prey fish for both species and the minimum size at which trout and charr were observed feeding on them was 13cm and 16cm respectively. Trout however were only observed to prey on charr when the trout attained a length of approximately 20cm a value which corresponds approximately to that of L. Rannoch and L. Ericht trout which appear to principally consume salmonids, the majority of which are probably charr.

Sticklebacks were very scarce in the two lochs, particularly in L. Rannoch where on no occasion were they caught in gill nets despite the use of small mesh sizes and by electrofishing the shallow margins of the lake. In L. Ericht, gill netting produced a single stickleback, suggesting that this species may be more abundant here which would explain its presence in four trout. Given the presence of a stickleback in the stomach of a single L. Ericht planktivorous charr of 150mm, it is probable that sticklebacks are sometimes consumed by smaller trout, although this was not observed. This was the only instance of piscivory in planktivorous charr from all three lochs apart from one individual from L. Tay. The lower frequency of piscivory and its onset at a larger size in trout is possibly due to trout of the size range analysed also being able to exploit littoral invertebrates. As well as being more abundant, these prey items are larger than *Pisidium* bivalves and chironomids which are the only prey items available in abyssal regions (Brinkhurst, 1974; Smith *et al.*, 1981; Lindegaard, 1992; Ward, 1992). In a study of two lakes in Quebec, Bérubé and Curtis (1986) similarly found that the charr in the lake with the poorest invertebrate prey abundance and inferior growth rates adopted piscivory to a larger extent and at a smaller size than the charr in the lake with the better prey abundance and superior growth rates. They too attributed this to the low profitability and high costs of searching for small prey in the invertebrate poor lake.

Differences in the prevalences of endoparasites reflected the differences in diet in the L. Rannoch charr and trout. Thus benthivorous charr which were almost never found to contain zooplankton had low numbers of individuals infected with

Diphyllobothrium sp., whereas planktivorous charr had the highest number of infected individuals. Similarly, a significantly higher number of L. Tay charr were infected with *Diphyllobothrium* sp. than were sympatric trout. Loch Ericht planktivorous charr and trout however, did not differ in the frequency with which they were infected with *Diphyllobothrium*, with the piscivorous charr having the highest frequency of infection. Given that this population was not found to consume zooplankton, the high frequency of infection is probably attributable to paratenic transmittion.

With regard to the length distribution of fish uninfected and infected with *Diphyllobothrium* sp., given that trout and piscivorous charr seldom consumed zooplankton, the occurrence of *Diphyllobothrium* in these fish groups must be a consequence of their consuming other fish infected with *Diphyllobothrium* sp. plerocercoids (Halvorsen and Wissler, 1973; Curtis, 1984). This is supported by the fact that *Diphyllobothrium* was not recorded in trout below length category mid point 220mm (except in two trout from L. Ericht), a length which approximately corresponds to the minimum size at which piscivory occurs. This was also the case with L. Rannoch piscivorous charr although not with L. Ericht piscivorous charr which acquired plerocercoids at a much smaller size. This supports the contention (assuming that sticklebacks are infected with *Diphyllobothrium*, direct evidence for which does not exist) that sticklebacks form part of the diet of piscivorous charr and trout in L. Ericht, which would enable them to adopt piscivory at a smaller size (L'Abée-Lund *et al.*, 1992). The higher frequency of piscivory in piscivorous charr (Fig. 6.6) than trout in L.

Ericht and Rannoch is reflected in the lower frequency of individuals of both trout populations infected with *Diphyllobothrium* over the corresponding size range (Fig. 6.10; 6.11) and the lower intensity of infection in trout than charr (Fig. 6.10). The higher intensity of *Diphyllobothrium* infection in L. Ericht piscivorous than L. Rannoch piscivorous charr (Fig. 6.8) may reflect that L. Rannoch piscivores are largely cannibalistic and therefore consume smaller conspecifics which are uninfected at the sizes at which they are preyed on whereas L. Ericht piscivorous charr consume sticklebacks which are likely to be infected even at small sizes (Curtis, 1984; Bérubé and Curtis, 1986). Planktivorous charr acquired plerocercoids at much smaller sizes as a result of feeding on zooplankton at small sizes.

The extent to which charr actively select various species of zooplankton is not known. Copepods were, however rarely identified in the diets of any charr. This was similarly noted by Halvorsen and Andersen (1984) who proposed that this was due to the relatively rapid digestion of copepods leading to them being under-represented. In the present study, the fact that *Daphnia* was abundant in stomach contents (data not presented) despite occurring at lower frequencies than both copepod species (Fig. 6.5) suggests that charr may actively avoid preying on copepods.

One interesting feature of the L. Rannoch and Ericht planktivorous charr is that although they consume zooplankton at the smallest sizes at which fish were caught, *Diphyllobothrium* plerocercoids are not evident until approximately

160mm which corresponds to an age of 2+ years. This was similarly observed by Halvorsen and Andersen (1984), who suggested that this was either due to smaller fish being able to entirely resist infection or due to infected fish suffering high levels of mortality and therefore not being recorded. However, another possibility is that smaller fish selectively avoid copepods. Halvorsen and Andersen (1984) determined that larger fish (for a given age) were more heavily infected with *Diphyllobothrium* than smaller fish due to larger fish having grown faster and having consumed a larger number of plankters, including copepods. The same process may operate in L. Tay charr which are the fastest growing (data not presented) and also are infected at smaller sizes than the other charr. Another important factor may be the degree to which copepods are themselves infected with Diphyllobothrium procercoids. Unfortunately no such data was obtained during this study.

The finding that both frequency and intensity of *E. truttae* were highest in the three trout populations is not unexpected given their habitat and diet preferences. *Gammarus* sp., the intermediate host of *E. truttae* was the third most frequently recorded prey item in L. Ericht trout. Although *Gammarus* was found in relatively few L. Rannoch trout, given that *Gammarus* sp. is predominantly a littoral animal (Brinkhurst, 1974; Smith *et al.*, 1981), that it was a more significant dietary component than dietary data suggested. Although L. Tay trout and charr were found to have consumed *Gammarus* in equal proportions, this prey item was only found in the diet of charr during the winter whereas trout are likely to forage on zoobenthos, including this prey item, throughout the year (Nilsson, 1960). Trout are therefore more likely to be exposed to infection by *E. truttae* than charr.

[1]CHAPTER 7 - A HERMAPHRODITIC ARCTIC CHARR FROM LOCH RANNOCH.

During a study of the reproductive status of Arctic charr *Salvelinus alpinus* (L.) sub-populations from Loch Rannoch internal examination of one individual revealed that one reproductive organ was hermaphroditic.The fish was of the planktivorous population (chapter 2; Adams *et al.*, 1998), had a fork length of 204 mm and was 4 years of age, a typical length at age for the population. This was the only such fish in approximately 1000 charr examined to date in this study.

The left gonad of the fish consisted anteriorly of 30 oocytes ranging from 1.2 - 1.4 mm diameter (Fig. 7.1). Histological examination of the gonads revealed that the remainder of the left gonad and the entire right gonad were functional testes with abundant spermatozoa and no further ovarian tissue. The oocytes were poorly developed (typical size range of Loch Rannoch charr oocytes immediately prior to ovulation = 3.0- 4.8mm diameter) and histological examination indicated that passage of the oocytes from their anterior location to the genital pore would not have been possible.

Many families of teleost fish, in particular the marine coral reef fish (e.g. Labridae, Scaridae, Serranidae and Sparidae), exhibit plasticity in sexual development in the wild (Francis, 1992). This does not appear to be the case in

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[1] This brief chapter is the basis of a paper: Fraser, D. 1997 A hermaphroditic Arctic charr from Loch Rannoch. Scotland. *Journal of Fish Biology* 50, 1358-1359.

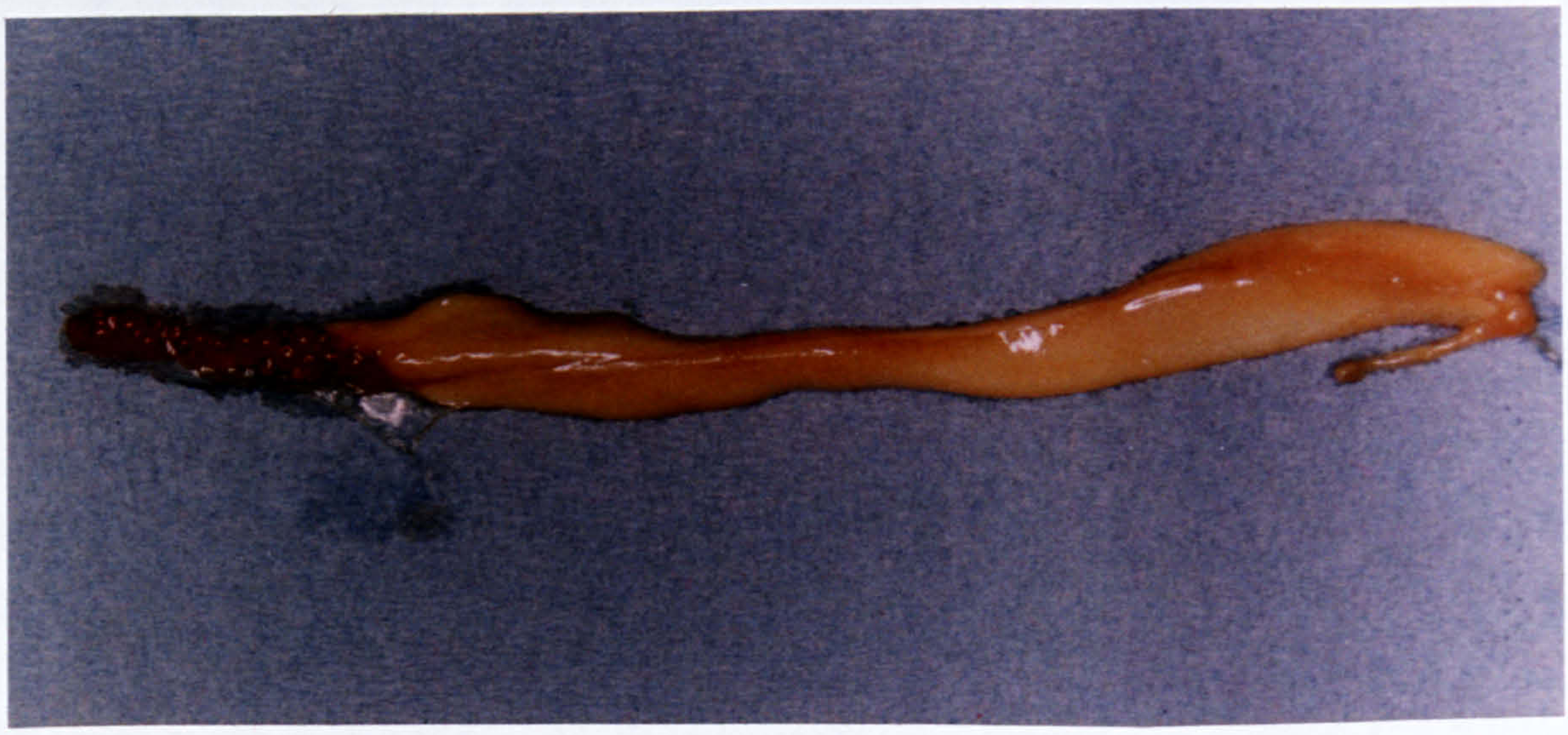

Figure 7.1 Hermaphroditic gonad (bottom) showing ovarian (left) and testicular (right) portions.

salmonids, where hermaphroditic individuals are only infrequently recorded, usually in large scale studies of populations (see references in Hutchinson, 1983).

Hoffmeister (1939) and Hutchinson (1983) each identified hermaphroditism in 3.7% and 2.6% of smelt *Osmerus eperlanus* (L.) in the Rivers Elbe and Thames respectively. These appear to be the only populations of salmoniform species in which functional synchronous hermaphroditism exists.

Recently there has been increasing evidence that alkylphenol polyethoxylates, a group of compounds widely used in industrial and agricultural processes, when introduced to the aquatic environment through sewage effluent are responsible for promotion of vitellogenesis in male fish resulting in feminisation of the reproductive organs (Sumpter & Jobling, 1995; Jobling *et al.*, 1996). Piferrer & Donaldson (1989) demonstrated that embryos of coho salmon *Onchorhynchus kisutch* (Walbaum) are highly sensitive to the actions of exogenous steroids during a period approximately 10 days either side of hatching. Loch Rannoch although situated in a sparsely populated, upland area does attract a large number of holidaymakers and so does receive effluent from holiday sites as well as from local settlements on its shores. The individual described here could have hatched out in the vicinity of such an effluent and therefore would be highly susceptible to phenotypic sex modification. Alternatively this condition could be the result of a rare spontaneous malfunction of the process of sexual differentiation.

[1]CHAPTER 8 - THE OCCURRENCE OF A CRUCIAN CARP IN LOCH RANNOCH.

The introduction into a water body of a fish species not previously occurring there and the subsequent establishment of that species is arguably one of the most serious, yet one of the most underestimated threats to freshwater fish communities (Mills *et al.*, 1994). In the North American Great Lakes for example, the ruffe *Gymnocephalus cernuus*, has recently joined a long list of European and Asian fish species that have been introduced that have established large, and often super-abundant, populations that have caused considerable ecological change (see e.g. Smith, 1971 on Sea Lampreys, *Petromyzon marinus*; Crowder, 1980 on Alewives, *Alosa pseudoharangus*; Richards *et al.* (in press) on ruffe), and economic loss (see Leigh, in press).

In the Great Lakes the vector for introduction of non-native species has been mainly through water transportation as ballast in cargo ships between North American and European and Asian ports (Busian, in press).

In Scotland, the relative simplicity of its fish communities make them particularly vulnerable to invasion (Case, 1990). As with North America,

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[1] This brief chapter is the basis of a paper: Fraser, D. and Adams, C. E. 1997 A crucian carp *Carassius carassius* (L.) in Loch Rannoch, Scotland: further evidence of the threat posed to unique fish communities by introduction of alien fish species. *Aquatic conservation: Marine and Freshwater Ecosystems* 7, 323-326.

Scotland has seen an increasing number of non-native fish species becoming established recently (Maitland, 1985). Unlike North America however, the principal vector seems to be translocation by anglers either as an attempt to establish new populations of sporting species or as a result of releases by anglers using non-native species as live bait to catch pike *Esox lucius* (Maitland, 1985, Adams, 1994). Of the Scottish lochs, Loch Lomond is the worst affected with five species having established themselves since 1980. In the case of the ruffe the rate of population growth has been dramatic (Adams and Maitland, in press) and the changes to the aquatic community fundamental (Adams, 1994; 1996).

Loch Rannoch, Scotland has a high conservation value as it contains three ecologically and morphologically distinct sub - populations of Arctic charr *Salvelinus alpinus* (Gardner *et al.*, 1988; Walker *et al.*, 1988; Adams *et al.*, 1998). Two of the three populations so far examined have been found to also differ genetically (Hartley *et al.*, 1992) . These can be considered as genetically pristine populations. The only other fish recorded in the loch are the brown trout *Salmo trutta*, the pike, the perch *Perca fluviatilis*, the minnow *Phoxinus phoxinus*, the three spined stickleback *Gasterosteus aculeatus,* the European eel *Anguilla anguilla* and the Atlantic salmon *Salmo salar* (Walker *et al*, 1988).

During a sampling visit to Loch Rannoch to capture spawning charr, as part of a study to examine life history strategies in the sympatric charr populations of the loch, a single crucian carp *Carassius carrasius* was caught. Although crucian carp has been recorded previously in Scotland (other than from Loch Lomond, to which it has been recently introduced (Adams and Mitchell, 1992)) it occurs only in a localised area in West Galloway in which at least four populations are known to exist (anon, 1997). Loch Rannoch is therefore the most northerly site in Scotland where it has been recorded from the wild.

The specimen from Loch Rannoch had clearly visible scars on both flanks, consistent with having been impaled on a hook as would have occurred if the fish had been used for live bait. Pike are locally abundant in Loch Rannoch and anglers are known to fish for this species. Thus it would appear that this specimen was an individual that had been used as live-bait but had escaped.

Evidence from Loch Lomond suggests that crucian carp may be reproducing successfully there (Adams, 1994). Therefore it seems possible, given the similarities in climate (annual temperature regimes) and that both offer significant habitat heterogeneity, some of which is likely to support crucian carp, that the species could also successfully reproduce in Loch Rannoch. Furthermore crucian carp are capable of surviving in much colder conditions than is generally perceived with populations known to survive in ponds in which a layer of ice forms for several months of the year (Hyvärinen *et al.*, 1985) and their ability to survive in anaerobic conditions (Hyvärinen *et al.*, 1985) is likely to make them less vulnerable to overwintering mortality and thus successful in a variety of aquatic habitats in Scotland.

The two most likely effects of the establishment of a crucian carp population to the Arctic charr populations are likely to be 1) competition for food: Adams *et al.* (1998) have shown that benthivorous charr consume (amongst other benthic invertebrates) predominantly chironomid larvae; this is also the case with crucian carp although they also consume cladocerans (Penttinen and Holopainen, 1992). 2) Changes in predator prey relationships. It is possible that the crucian carp could provide a food source for piscivores such as pike, thus increasing the pike population and increasing the predation pressure on charr.

Due to the isolated nature of landlocked freshwater fish populations, they have evolved in response to very exacting circumstances according to variation in habitat. Changes in that habitat however subtle are liable to exert novel selection pressures on indigenous populations with unknown consequences.

In view of the increasing frequency of unwanted fish introductions, the fact that introductions once made are irreversible and increasing knowledge of their impact, it is a matter of some urgency that legislation is introduced making such translocations of fish illegal (Maitland, 1996). In addition to this it is important that the public-and in particular anglers, aquarists and fish farmers -are educated to regard such indiscriminate translocations as unethical (Maitland, 1987) and that the issue of fish translocation receives a higher profile in the context of aquatic communities than it has hitherto.

CHAPTER 9 - GENERAL DISCUSSION

9.1 Summary of findings

1) Does the benthic morph described by Walker *et al.* (1988) consist of two distinct morphs? If so what is the basis of this segregation? (chapter 2)

Morphometric analysis of eleven size corrected morphometric variables clearly identified two cryptically coloured morphs (previously known as the benthic morph (Walker *et al.*, 1988)). The discontinuity of morphology was associated with different spawning sites, indicating that these two morphs are reproductively isolated. Dietary analysis indicated that the two cryptically coloured forms differed in their foraging specialisations. Thus, the morph spawning at the mouth of the River Gaur consumed benthic invertebrates throughout its size range whereas the morph which spawned in the Dall bay region showed similar dietary preferences until a size of approximately 16cm was reached, whereafter it consumed predominantly other fish. The terms benthivorous and piscivorous were therefore adopted for these morphs. Morphometric and dietary data confirmed the status of the pelagic morph described by Walker *et al.*, 1988. This morph was termed the planktivorous morph.

2) How do the morphs differ in terms of population structure and life history strategies?(chapter 5)

The three morphs exhibited large differences in a number of life history traits

Piscivorous fish were the longest lived (maximum age of 17+ years) followed by benthivorous and planktivorous fish (11+ and 7+ respectively). Piscivorous females matured at 1+, as opposed to planktivorous and benthivorous females, which matured at either 2+ or 3+. Differences in length at age were detectable from an early age with piscivorous fish growing slowly but maintaining growth throughout their lifetimes. Planktivorous and benthivorous fish grew fast initially but reached an asymptote after 3+ years. The asymptotic size (L_∞) determined by the Von-Bertalanffy growth equation of planktivorous fish (216mm) was smaller than for benthivorous fish (238mm) which was in turn smaller than for piscivorous fish (404mm). Reproductive output in terms of both fecundity and egg mass was highest for benthivorous fish, followed by planktivorous then piscivorous individuals.

3) Do the charr of Loch Ericht and Tay exhibit polymorphism? If so, what is its basis? (chapter 3, chapter 4)

Using the same morphometric procedure used to discriminate the L. Rannoch morphs, two distinct charr morphs were identified from L. Ericht. Dietary data indicated that one was a planktivorous morph and the other was a piscivorous morph. Length at age also differentiated between the two morphs. Loch Tay charr were found to be monomorphic although two individuals were found to differ in morphology and diet from all other fish. This could have been due to long term foraging specialisations although due to the small number of fish concerned no conclusions could be made.

4) How do the charr populations in the three lochs examined compare morphometrically and do populations from different lochs which occupy similar trophic niches have similar morphologies? (chapter 4)

PC1 of a principal components analysis (45% of variance) indicated that both L. Ericht and Rannoch piscivorous morphs were broadly similar in morphology with large heads and jaws and differed from all the other morphs which were themselves broadly similar in morphology and had relatively small head and jaw features.

5) How are the charr morphs and brown trout segregated in the three lochs investigated in terms of habitat utilisation, diet and patterns of parasite infection? (chapter 6)

In all three lochs examined, brown trout occupied the littoral zone whereas charr mainly occupied deeper water and the pelagic zone. In L. Rannoch and Ericht piscivorous charr were caught at significantly greater depths than trout and planktivorous charr.

Planktivorous charr (including L. Tay charr) consumed zooplankton (almost exclusively cladocerans) when abundant and piscivorous charr consumed predominantly profundal benthic invertebrates such as *Pisidium* bivalves and chironomids and almost exclusively fish above a fork length of 16cm. At all times of year and in all lochs, trout depended on a broad range of prey items, in particular trichoptera larvae and terrestrial insects.

Planktivorous charr were infected with plerocercoids of *Diphyllobothrium* sp. from an early age as this parasite is transmitted by ingestion of infected copepods. L. Rannoch benthivorous charr exhibited low levels of infection with this parasite as planktonic zooplankton was not part of their diet. Amongst piscivorous charr and trout, individuals infected with *Diphyllobothrium* were only present at fork lengths above the minimum size at which they exhibited piscivory indicating that infection was due to paratenic transmission rather than ingestion of copepods. All trout populations harboured high numbers of the acanthocephalan worm *Echinorhynchus truttae* in relation to charr. This parasite is transmitted by ingestion of the amphipod *Gammarus* sp. Given that *Gammarus* occurs mainly within the littoral zone trout are more susceptible to infection than charr.

9.2 Discussion of findings

Basis of trophic partitioning in charr populations

From a review of the literature, it can be seen that the basis of trophic partitioning in lakes differs greatly and can be described by the following categories. These four categories show a progression from no differentiation to complete reproductive isolation:

1) Monomorphic populations which exhibit no such partitioning.

2) Monomorphic populations where individuals irrespective of size appear to have long term trophic and habitat preferences (e.g. Curtis *et al.*, 1995; Knudsen, 1995;

Knudsen *et al.*, 1996; Bourke *et al.*, 1997), and thus may exhibit trophic specialisation as a polymorphic population.

3) Polymorphic populations where morphs are the result of different developmental routes as is the case with the charr of Lake Vangsvatnet, Norway (Jonsson and Hindar, 1982) or ontogenetic stages (e.g. Klemetsen *et al.*, 1985; Riget *et al.*, 1986)

4) Polymorphic populations where morphs are genetically distinct and largely or wholly reproductively isolated, as seems to be the case with Thingvallavatn (Sandlund *et al.*, 1992).

The reason for the existence of any degree of trophic specialisation is the vast difference in the nature of benthic and planktonic prey types. Schutz and Northcote (1971) and Werner *et al.*, (1981) have shown that in order to exploit these prey types efficiently, quite different feeding behaviours and strategies are required. Thus when bluegill sunfish were introduced into a pond with abundant zooplankton and zoobenthos, fish either specialised on one prey type or another with few fish consuming both. Laboratory feeding experiments indicated that bluegills required a period of time to learn how to utilise a prey type efficiently. Once a fish has learned the appropriate behaviour to exploit a particular prey type efficiently, this behaviour will be inefficient in exploiting the other prey type. Similarly, efficient planktonic and benthic feeding require quite different morphological adaptations (Lavin and McPhail, 1986; Schluter, 1993; Walker, 1997). In phenotypically plastic species such as bluegill sunfish, threespined sticklebacks and Arctic charr, a population is likely to contain individuals which are morphologically slightly better adapted to benthivory or planktivory. This, combined with the different behavioural requirements of benthivory and planktivory and of reduced intraspecific competition of individuals at the extreems of the range of morphological variation (Schluter, 1994) will further reinforce foraging specialisations (Ehlinger, 1990). Poorer profitability of a generalist foraging strategy (Werner *et al.*, 1981) and of being morphologically intermediate (McPhail, 1994; Schluter, 1994) will provide the basis for disruptive selection and hence assortative mating (Rundle and Schluter, 1988) and eventually complete reproductive isolation.

It is not clear why the populations exhibiting discrete trophic partitioning (classes 3-4 above) differ in the degree to which they have an associated population differentiation. Factors such as circannual stability of each trophic resource and availability of habitats which enable reproductive isolation may be important. Alternatively these four stages may represent a progression in the speciation process with class 2 representing an early stage of population differentiation and class 4 representing the most advanced situation. Certainly the charr of L. Rannoch and probably L. Ericht fall into the last group with morphometric, trophic, reproductive and in the case of L. Rannoch, genetic discreteness being demonstrated. A small percentage of L. Tay charr appeared to forage on zoobenthos during a time of plankton abundance. These fish also exhibited uncharacteristic pale colouration and slight morphological differences from the majority of the plankton feeding charr. Samples of these fish were too small to make any firm conclusions but it is possible that L. Tay individuals specialise on either benthos or plankton feeding with no or little morphological diversification and thus correspond to the second group. It is also suggested that the reason for the absence of a benthic feeding morph or at least the extreme scarcity of benthic feeding individuals is a consequence of that niche being occupied by eels. Little attention has been paid to eels in ecological studies of freshwater fish, mainly due to their not being susceptible to capture by gill net and their importance in trophic interactions has therefore been underestimated. A more extensive study of charr and other fish species in L. Tay certainly seems to be merited.

Evolutionary origin of polymorphisms

The question as to whether the charr morphs within L. Rannoch (and Ericht) are sympatrically or allopatrically derived is still unresolved. However, given the large degree of morphological differences among the forms within each loch it must be concluded that most of the divergence in trophic morphology has resulted since colonisation. This does not preclude different ancestral origins of the different forms, but given the relative morphological uniformity of anadromous charr throughout the species geographical range and indeed anadromous salmonids as a whole (fusiform with small heads in relation to body length (Johnson, 1980)), if two ancestral invading forms did colonise the lochs, they must have been morphologically similar and possessed anadromous type morphologies. Such uniformity in anadromous populations and variability in freshwater populations is also observed in the threespined stickleback (McPhail, 1994) and occurs due to the relatively homogenous nature of the marine environment (Nicieza, 1995). Similarly, adaptations such as the differential abilities of planktivorous and piscivorous charr to evacuate their swim bladders could only have evolved since colonisation of a lacustrine habitat. In order for the genetic integrity of two or more ancestral forms to be carried through to the present day, the forms need not necessarily have been morphologically differentiated. Differences in reproductive characteristics such as time of spawning, place of spawning e.g. riverine or lacustrine or conspecific mating preferences would enable genetic isolation to be maintained. The situation in L. Windermere is of particular interest in this respect in that four reproductively isolated populations exist with little associated morphological differentiation (Partington and Mills, 1988), although there is no indication as to whether these are sympatrically or allopatrically derived.

The only genetic study carried out on the charr populations under investigation here was conducted by Hartley *et al.* (1992). The conclusion of Hartley's study was that Loch Rannoch had been colonised by two invading forms. However, this was based on only a single polymorphism of the DNA *Hin*dIII variant, the origin of the benthic fish used is uncertain i.e. whether they were the piscivorous morph or the benthivorous morph and the sample size was small. There is a growing body of genetic (Hindar *et al.*, 1986; Danzmann *et al.*, 1991; Taylor *et al.*, 1996; Wood and Foote, 1996; Pigeon *et al.*, 1997) and experimental (Schluter, 1994) evidence that sympatric morphs of salmonid fish are derived from intralacustrine divergence of a common post glacial invading ancestor. Even amongst cichlids of the African rift Lakes, long thought to have arisen from allopatric processes

(Greenwood, 1965) speciation processes are now thought to have occurred within the last 12 000 years as recent evidence indicates that prior to this the lake was dry (Johnson *et al.*, 1996). Ten thousand years is also the time scale that intralacustrine speciation processes would have to have occurred in charr populations given the extent of the polar ice cap prior to this. Although evidence for allopatrically derived lineages of salmonids does exist (Hindar *et al.*, 1986; Wilson *et al.*, 1996; Pigeon *et al.*, 1997), generally, the present day distributions of these different lineages do not overlap and so these are unlikely to be the origin of sympatric morphs. One exception to this is the study of the sympatric brown trout morphs of Lough Melvin by Hynes *et al.* (1996), which indicated that all three morphs were derived from separate invading ancestral forms. Given the discovery of a third morph of charr in L. Rannoch, the discovery of two morphs in L. Ericht and the existence of a very similar loch in the same catchment (L. Tay) whose charr do not exhibit polymorphism, the charr in these lochs provide excellent subjects for the study of evolutionary processes in polymorphic charr and merit further genetic analysis.

Spatial and temporal segregation and the evolution of trophic specialisation

The temporal differences in peaks of spawning activity among the L. Rannoch morphs were not studied systematically, although sampling in three successive years indicated that there was little if any difference at least between the planktivorous and benthivorous morphs. Many fewer piscivorous charr were caught and information regarding their time of spawning is not as comprehensive as for the other two morphs. While most ripe piscivores were caught at the same time as ripe benthivores and planktivores, several ripe piscivorous fish were caught in November when virtually all benthivorous and planktivorous charr were spent. Furthermore, two ripe males were caught during March. This suggests that while there is temporal overlap in spawning, piscivorous fish spawn over a longer period than the other morphs. This could be due to the fact that at the depth at which piscivores occur, temperature and light levels will be very constant over time (Smith *et al.*, 1981). This may prolong the spawning period of piscivores in two ways: 1) environmental cues to spawn will be less well defined 2) suitable temperatures for egg incubation will exist over a longer time period. Spatial segregation between the piscivorous and benthivorous morphs at spawning time and indeed throughout the year, was almost absolute, with piscivores occupying the east basin and benthivores confined to the smaller west basin and spawning in the mouth of the afferent River Gaur and possibly the smaller afferent River Ericht which also enters the loch in the west basin.

Few spawning planktivorous individuals were caught in the west basin, this morph being mainly confined to the east basin, together with the piscivorous morph. Depth segregation between these two morphs was evident, although it is likely that some spatial overlap existed. Since no apparent hybrids between piscivores and planktivores were ever caught, it is likely that some degree of assortative mating occurs between these two morphs. An attempt was made to investigate this by transporting wild caught pre-spawning fish to the semi-natural environment of an artificial flume tank at the University Field Station, Rowardennan where behavioural interactions between the two morphs could be observed. Problems encountered with the survival of fish, particularly piscivores (perhaps unable to adapt to the depth change) and female planktivores, all of which died within days of capture, prevented this from being successfully undertaken. However, tank reared L. Rannoch charr successfully spawned when introduced to the flume tank. Although it was not possible to obtain sufficient data to draw any conclusions about behavioural interactions, this indicates the feasibility of pursuing this aspect of their reproductive behaviour. It is posible, given that the charr exhibit spatial segregation in spawning, that morph specific mate preferences are less well developed than in sympatric stickleback morphs where both morphs utilise the same spawning area and morph specific mate preferences are strong (Rundle and Schluter, 1988).

The spawning behaviour of the piscivorous morph is likely to be of particular interest given the great size range over which spawning individuals occur which is likely to result in size assortative mating which is liable to be reinforced by the fact that small spawners are potential prey for larger individuals.

Although north and south basins of L. Windermere appear to further separate spring and autumn spawning charr there (Partington and Mills, 1988), the isolating mechanism of the two basins in L. Rannoch appears to be unique in documented charr polymorphisms. Not only are the profundal charr (i.e. the piscivores and benthivores) reproductively isolated as a result of each inhabiting their respective basins (reproductive isolation being further reinforced by the adoption of riverine spawning in the west basin), but each utilises different trophic resources and differs in its morphology correspondingly as a result of the respective biotic conditions in each basin. Although each utilises the profundal zone, the bathymetry of each basin is likely to result in different benthic macro-invertebrate communities. Benthic invertebrates become impoverished in terms of number of species and individuals with increasing depth (Smith *et al.*, 1981). Thus, the maximum depth of the west basin is 30m. This constrains the depth at which charr can occur. The east basin has a maximum depth of 115m and piscivorous fish generally are not caught in high numbers at depths shallower than 30m. Furthermore, the west basin is the only area of the loch in which significant areas of aquatic macrophytes occur (Campbell, 1971). The two basins therefore function like two lochs, the west basin being richer as a result of its relative shallowness and from the input of allochthonous material from the two afferent rivers, and the east being relatively impoverished, primarily as a result of a lower proportion of its area being shallow. The west basin has therefore selected for a benthivorous specialist whereas in the east basin the impoverished benthic fauna selects for the adoption of piscivory (Campbell, 1979).

It should be noted however that prior to the switch to piscivory in the piscivorous morph, its diet is similar to the benthivorous morph. Thus it is likely that the piscivorous morph is morphologically less well adapted to utilise benthic invertebrates than the benthivorous morph. This may partially account for the poorer growth in the piscivorous morph in relation to the benthivorous morph in early years during which time it is dependent on benthic invertebrates. Only limited studies of the relative feeding efficiencies and foraging behaviours of the

L. Rannoch morphs have been carried out to date (Adams and Huntingford, unpublished data) and further studies of this nature are required.

With respect to the two basins of L. Rannoch, the nature of the west basin is atypical of large glacial ribbon lakes of the Scottish Highlands in that it is shallow and has significant amounts of aquatic macrophytes. In terms of habitat, the east basin and L. Ericht are comparable and this is reflected in the fact that ecologically and morphologically, the L. Ericht profundal morph corresponds to the Rannoch piscivorous rather than benthivorous morph.

Unlike the two instances of trophic polymorphism described here, throughout Scandinavia, all documented charr polymorphisms consist of a dwarf benthic form, these exhibiting similar ecologies and morphologies throughout their range (Hindar *et al.*, 1986). It is therefore possible that biotic differences between lakes in Scotland and Scandinavia select for different trophic specialisations.

Significance of colouration

One of the most distinguishing features of the profundal morphs described in this thesis (L. Rannoch benthivores and piscivores and L. Ericht piscivores) was their pale colouration and the presence of parr marks at all sizes. The other three forms which are all pelagic planktivores exhibit red / orange colouration ventrally and black colouration dorsally, the red colouration being a consequence of the carotenoid content of their zooplankton diet (Hatlen, 1997). Other planktivorous forms of charr have been documented as having silver, smolt-like colouration in addition to red ventral colouration (e.g. Sandlund *et al.*, 1992). A possible explanation for the differing colouration of the pelagic charr described here is that Scottish lochs are heavily stained by peat colloids and in order to be less conspicuous to potential predators, charr must be correspondingly dark. Pale colouration and the presence of parr marks is also a feature of dwarf charr reported elsewhere (e.g. Hindar and Jonsson, 1982; Nilsson and Filipsson, 1971). Colouration has been demonstrated to be of great importance in recognition of individuals of the same species in cichlids where morphologically similar, closely related species also occur (Seehausen *et al.*, 1997) and may also be of importance in recognition of charr of the same morph. In some charr populations where morphs appear not to belong to separate gene pools, mature dwarf charr which exhibit pale colouration and parr marks may use this colouration for the opposite purpose in that they employ a sneaking strategy by masquerading as juveniles and attempt to spawn with normal females (Hindar and Jonsson, 1982; Svedang, 1992).

Possibility of further polymorphic populations

The extent to which polymorphism occurs in other Scottish lochs is unknown. If piscivorous morphs similar to those described here were to occur in other lochs, given the great depth at which they occur, and in the case of L. Ericht, their extreme scarcity, it is likely that they have been overlooked by anglers and even fisheries biologists employing gill nets. A large scale survey of Scottish lochs and Irish loughs recently completed (Adams, unpublished data) indicated that no charr corresponding to the piscivorous morphs described here were found. However, a great many lochs remain uninvestigated. Reports in the angling press indicate in recent years that a number of charr each of at least 2.5kg have been caught in L. Ness by salmon anglers. To date other reports of charr from L. Ness have described a planktivorous form typical of those described in this study (Dr Colin Bean, pers comm). Given that the maximum size that planktivorous charr can obtain in such lochs is small, it seems that these reported fish must belong to a piscivorous morph.

Conservation

This situation in L. Rannoch stresses the importance of identifying individual stocks of the same species in order to conserve biodiversity (Behnke, 1972; Ricker, 1972; Ferguson and Taggart, 1991). Although the piscivorous morph occurs in large numbers throughout most of the loch, the benthivorous morph has a very localised distribution and spawning site. This makes the benthivorous morph particularly vulnerable. Furthermore, while the east basin of the loch is likely to be unfavourable to the establishment of non-salmonid fish species, the west basin is likely to be more favourable in this respect for reasons outlined previously. The introduction of alien fish species such as the crucian carp or the Ruffe *Gymnocephalus cernuus* is thus a very real threat to the charr of L. Rannoch (Fraser and Adams, 1997; Adams and Maitland, in press) in particular the benthivorous morph. Much of the Tay catchement, including L. Rannoch is subject to a brown trout protection order which requires anglers to obtain permission prior to commencing angling. Loch Rannoch is fortunate in that this offers the opportunity for angling to be policed and a livebait ban to be enforced.

At present no such ban exists but in the absence of legislation to outlaw fish translocations on a national basis it is recommended that where such protection orders exist, local bans are put in place.

Another potential threat is that of genetic alteration of these populations by introduction of charr from other populations. Such a potential threat comes in the form of charr aquaculture which is being carried out on a small scale in a small number of locations in Scotland. Escapes of adult salmon from cage rearing facilities occur on a frequent basis. Escapee adult fish ascend nearby rivers and spawn with the wild salmon of that river. This has caused much concern that the river specific adaptations of the wild stock will be lost due to the genetic input from the farmed fish (Verspoor, 1997). In the case of the polymorphic populations described here such interbreeding would not only compromise the pristine genetic composition of the morphs, but would possibly lead to the breakdown of reproductive isolation amongst the morphs. Furthermore, given the much larger degree of variability and local adaptation in Arctic charr than Atlantic salmon, the implications of interbreeding are therefore likely to be far greater for Arctic charr. Such a threat could also come in the form of stocking for fisheries enhancement. Stocking of Arctic charr for such purposes has not been carried out in Scotland to date although at least one fish farm is known currently to be advertising Arctic charr for sale for stocking purposes. The closely related brook charr *Salvelinus fontinalis* has, however, been introduced into a handfull of Scottish lochs (Maitland and Campbell, 1992). Given that introduced brook charr have been found to naturally hybridise with native Arctic charr (Hammar *et al.*, 1991), introductions of this species into water bodies containing original populations of Arctic charr should be avoided (Hammar *et al.*, 1991). Indiscriminate stocking of a large number of freshwater bodies with brown trout has occurred throughout this century (Maitland and Campbell, 1992) with the result that very few brown trout populations can be said with certainty to be genetically pristine. At present Arctic charr populations in the UK can however be said to be genetically pristine. Charr farming need not pose a threat to the pristine genetic nature of UK charr populations provided that farms use fish endigenous to the water body in which cage rearing facilities are situated and that farms are not allowed to be established on lochs in which polymorphic populations exist. The import of commercial strains from abroad which are derived from anadromous populations is a particular risk and should be avoided

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